An investigation of the potential threat of habitat fragmentation on some Northern Region bird species

(submitted as part of a final report for contract #53-0343-2-00207)

Richard L. Hutto

Division of Biological Sciences
University of Montana
Missoula, MT 59812
em:hutto@selway.umt.edu

INTRODUCTION

As an amendment to USFS Northern Region landbird monitoring contract # 53-0343-2-00207, I was asked by Fred Samson to provide a summary document outlining which Northern Region bird species might be threatened by habitat fragmentation. Specifically, I was asked to investigate whether information from our long-term monitoring points might be useful in examining the influence of landscape context (especially patch size) on bird presence, and if so, which species might be so affected. This report is meant to serve as a summary of our methods of analysis, and a summary of the findings that resulted from this effort.

METHODS

To evaluate whether landscape condition (specifically, patch size) influences the probability of occurrence of a bird species above and beyond the influence of local-scale conditions, one should evaluate the effects of both local- and landscape-scale variables simultaneously so that local-scale conditions can be held constant statistically. As an initial step in this process, we examined landscape variables in a univariate context, but we controlled for

local-scale habitat conditions by dividing the data into three broad habitat categories, so that all points used in an analysis were situated in potentially occupiable habitat, and the relatively isolated effects of landscape context could then be examined.

We used our existing habitat relationships models (see Hutto 1997 for project design, point count methods, and bird-habitat relationships) to select species that were relatively restricted to either (a) conifer forest, (b) riparian, or (c) open-land cover types. These three broad cover type designations include several finer resolution cover types that both we (Hutto and Hoffland 1996), and the University of Montana Spatial Analysis Lab previously defined (see Table 1). To produce the bird-habitat associations illustrated in Hutto (1997) and included here as part “d” in Figures 5-24, we excluded points that had more than one cover type within 100 m (edge points) to ensure that any species detected at a point actually occurred in (was associated with) the habitat of interest. All riparian points were included, however, because most all of those points had another major cover type within 100 m.

Total bird species pool--Of the 186 bird species detected on long-term monitoring points between 1992-1994, 106 species were detected close enough (within 100 m) and frequently enough (on 15 or more points) to construct meaningful habitat-relationships models (see Hutto 1997). Of those 106 species, we included any one that occurred on at least 20 points in any one of the three cover types defined above, which left a total of 76 species with enough observations to conduct landscape analyses (Tables 2-5).

Defining riparian-restricted species--A bird species detected at a "riparian" point may have actually occurred in a different habitat within 100 m of the point. This means that many broadly distributed species occurred at riparian points due to their ubiquity in other habitats. Therefore, a riparian-restricted species was defined as one that was much (at least five times)

more common at riparian points than in any other cover type. As an index of the level of riparian dependency, we calculated the percent occurrence of each species at riparian points divided by the percent occurrence at all other points combined. Those species that were at least five times more likely to occur in riparian areas than elsewhere were deemed to be riparian-restricted species (Table 2). Five additional species (with index values between 3 and 5) plus Black-capped Chickadee (index=2.94) and Red-naped Sapsucker (index=2.06) were included even though they occur in shrubby clearcuts as well as riparian areas (Table 2).

Defining conifer-forest species--After the riparian species were selected, from the remaining species we selected those that were relatively restricted to conifer habitats, using an index calculated as the percent occurrence of each species at conifer points divided by the percent occurrence at open points. We considered all species with a "conifer index" greater than 1.25 to be conifer-dependent, although the species with an index below 2.00 tend to prefer very open forest or occur across a variety of habitats (Table 3).

Defining open-land species--Species relatively restricted to open land were selected as those with a conifer index less than 0.25, although only the seven species with an index of 0.00 (those never detected in conifer habitats) were truly restricted to open country (grassland, sagebrush, agriculture) (Table 4). Species with index values between 0 and 0.25 tended to be species of shrublands and open forests; they were detected in open land points because the GIS database included clearcuts and forest types with less than 15% canopy cover in the "open land" category (Table 4).

Unclassified species--Thirteen birds species were fairly broadly distributed across the three cover type categories (Table 5). We did not include them in our landscape analyses because the concept of patch size and shape are less meaningful to species that are broadly

distributed across available vegetation types.

Landscape variables--The effect of landscape context on each species was analyzed using the subset of points that fell within the cover type within which the species was relatively restricted (either conifer, riparian, or open land). All points within each cover type group were used regardless of their proximity to the edge of that cover type. The subset of points included in the analysis of a particular cover type included those that the GIS database indicated fell within that cover type. For the conifer group, we further refined which points were included by selecting only those points that our own field data also indicated were situated within a conifer cover type. Sample sizes were not sufficient for the other two habitat subsets to allow us to eliminate points for which there was disagreement between our own and the GIS database.

We programmed the computer to look at a 1-km-radius circle surrounding each point. Within this circle we calculated several landscape variables from the GIS database. We used two different cover type classifications, depending on the particular landscape variable. Two variables were calculated on the basis of cover types that were merged into three general categories (conifer, riparian or open land): (1) the proportion of the 1-km-radius circle that was filled by potentially occupiable habitat (conifer, riparian or open land), and (2) size of the habitat patch within which the point fell (the area of contiguous coverage of the same general cover type as at the point). The other variable was a measure of fragmentation based on a cover type classification scheme involving the 15 cover types in the right column of Table 1: (3) edge density (m/ha) within 1-km-radius circle.

Landscape analysis--We converted the bird data to presence or absence of each species at each point, and used logistic regression to determine the degree of association between each species and each landscape variable. For display purposes, each landscape variable was

categorized to create bar graphs that depicted the percent occurrence of each species at discrete levels of each landscape variable (within the appropriate habitat group). For the purposes of analysis, we lumped some categories to achieve sufficient sample sizes within each.

RESULTS

The landscape analyses in this report incorporated bird counts at 6000 points in western Montana and northern Idaho (thus excluding the Custer NF points used in the GTR), conducted between 1992 and 1994. These included 3769 conifer points, 525 riparian points, and 1706 open points.

The typical landscape surrounding a sample point was not a homogeneous patch of one of the three cover type categories. Rather, the area surrounding each point consisted of a mixture of cover types (Figure 1), with a mean of 36 separate cover type patches per 1-km-radius circle around the point. Although often highly skewed, the range of values available for our landscape variables was great, making our particular collection of sample points well suited for a landscape analysis (Figures 2-4).

The three landscape variables were somewhat correlated with one another (Table 6), but not strongly enough to suggest that they were entirely redundant measures. Thus, patch size and the percentage of the cover type of interest within a 1-km-radius area around the point are the better measures of area dependency, while edge density is a better measure of how broken up or fragmented the landscape is around the point.

Conifer-restricted bird species--The probability of occurrence for seven of the 31 conifer-restricted species was significantly positively correlated with the percentage conifer

forest within the 1-km-radius area surrounding the point and with the size of the conifer forest patch within which the point was situated (Table 7; Figures 5-11). Their probability of occurrence was also negatively correlated with edge density in the 1-km-radius area surrounding the point (Table 7). Although percent conifer and patch size were negatively correlated with edge density (Table 6), the correlations are weak enough to suggest that these seven species may be sensitive to both area effects and fragmentation effects in the conifer forest landscape. The occurrences of another eight conifer-restricted species were significantly negatively associated with either percent conifer forest surrounding the point or with patch size, and the occurrences of seven species were positively correlated with edge density (Table 7).

Riparian-restricted bird species--Six riparian-restricted species were positively associated with the percentage of riparian cover in the 1-km-radius circle surrounding the sample points (Table 8; Figures 12-17). Three of these plus two other species were also positively associated with edge density (Table 8). Edge density was positively correlated with the percent of riparian cover among riparian points (r= 0.51; Table 6). Unlike the situation for conifer points, where relatively large conifer patches tend to have little edge within the 1-km-radius circle surrounding the sample point, landscapes with a lot of riparian lands still tend to have a lot of edge. Thus, “edge density” may not be a very good measure of fragmentation of the riparian area itself. No riparian-restricted species was significantly negatively associated with any of the three landscape variables, and there were no significant associations with patch size (Table 8).

Bird species restricted to open land--All of the "open land" species were very strongly associated with all three landscape variables (Table 9; Figures 18-24).

DISCUSSION

Some authors have suggestd that western bird species might not be sensitive to landscape fragmentation because western conifer forests are born of fire regimes that have led to naturally fragmented landscapes (Hejl 1992, Hutto et al. 1993, Hejl et al. 1995, but see Miller et al. 1996, Reed et al. 1996). Nonetheless, our results suggest that forest-dependent species may not occur as commonly in small as in they do in larger forest patches. The fact that we ran multiple univariate analyses suggests that some of the significant associations are statistical artifacts due to chance alone. However, most of the species that appear to be patch-size dependent (e.g., Townsend's Warbler, Swainson's Thrush) are species whose biology suggests that the results are not a statistical artifact. The important point is that we have isolated a group of the most likely candidates for forest patch-size dependency; the issue can now receive more more focussed study, with special attention given the mechanism behind the origin of such nonrandom distribution patterns.

The strong association between occurrence and patch size for all of the open-land bird species may be due to the inclusion of clearcuts and other shrubby habitats in the "open land" habitat grouping. That is, points that fell within clearcuts and other shrubby habitats were classified as open-land points by the GIS classification scheme because such differences cannot be distinguished through remote sensing. Because such shrublands are inappropriate for most open-land (predominantly grassland) bird species, and because shrublands are more likely to exist in smaller patch sizes than grasslands (Figure 25), this may have biased the apparent response of grassland species to the landscape variables. Once we can better tease apart the various open-land categories with a more refined GIS classification scheme, we can conduct an analysis with points that were more clearly restricted to the open lands and better investigate the effects of patch size on open-land bird species.

The low sample sizes for riparian species severely compromise our ability to evaluate the effects of landscape context on bird presence. This attests to the need for more focused studies on riparian habitats, both in the streamside riparian habitats common on National Forest lands, and in the more extensive cottonwood bottomlands, which are critical to many of these species but are not covered well by the positioning of our long-term monitoring transects.

Caveats associated with this analysis--We have come to recognize several problems inherent with landscape-level analyses in general, and more specifically, based on landscape-level information extracted from a remotely sensed GIS database. First, a potentially suitable or occupiable "patch" for any given species is difficult to define and should not be taken lightly. Conditions that constitute an edge to one species (or its predators or parasites!) will cetainly not constitute an edge to another. How different must cover types be to constitute distinct "types"? If one cannot define that objectively, then measures of patch size and so forth will be meaningless. We suspect that the most meaningful analyses were produced for the bird species that were most strongly restricted to one of the three cover types, but it will always remain a task for the data analyst to use his or her knowledge of the biology of the species to decide how to best describe units of habitat that are uniformly suitable for a given species...a daunting task.

Secondly, even if we can agree on what constitutes the edge of suitable conditions for a given bird species, there is the problem of accuracy in identifying and mapping acceptable and unacceptable cover types to enable the calculation of landscape indices. If patches of shelterwood forest, for example, are unacceptable to a bird species, but are classified with other forest types because they cannot be distinguished from other forest types through remote sensing, then any measure of patch size, fragmentation, or whatever, will be innaccurate to the extent that these forest types are intermixed.

Thirdly, there is the ever-present problem of confounding variables in landscape analyses. For example, many of the apparently landscape-sensitive conifer-restricted species are more abundant toward the western end of the region (Idaho and northwestern Montana), which is dominated by dense, mesic forests. If these forests, or that part of the region, tend to have less patchiness than more eastern areas, then the landscape association may be an artifact of these confounding problems. Certain conifer forest types are also more likely to be associated with certain landscape configurations, so the effect of landscape vs. local-scale species composition will need to be teased apart with multivariate techniques before one can conclude that it is the landscape configuration per se to which several bird species are responding.

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Table 1. Landbird Monitoring Program (LMP) and UM Spatial Analysis Lab (SAL) cover types included within each of the three general habitat groupings used in landscape analyses.

	LMP cover types	SAL cover types
Conifer:	CEDAR-HEMLOCK	MIXED ALPINE
	SPRUCE-FIR	MIXED MESIC
	LODGEPOLE	MIXED SUBALPINE
	MIXED-CONIFER	MIXED XERIC
	DOUGLAS-FIR	MIXED CONIFER/BROADLEAF
	PONDEROSA PINE	
	GROUP SELECT	
	SHELTERWOOD	
	SEED TREE	
Open:	CLEARCUT	GRASSLANDS/SHRUBLANDS
	SAGEBRUSH	AGRICULTURAL
	GRASSLAND	BARREN LAND
	AGRICULTURAL	ALPINE MEADOW
Riparian:	MARSH, WETLAND	FORESTED RIPARIAN
	RIPARIAN SHRUB	NON-FORESTED RIPARIAN
	COTTONWD/ASPEN	BROADLEAF
Excluded:	POST-FIRE	STANDING BURNT/DEAD TIMBER
	RESIDENTIAL	URBAN/DEVELOPED
		WATER

Table 2. Bird species relatively restricted to riparian cover types, as indicated by a "riparian index" (see Methods). Under "Cover type", the percent occurrences of each species in the 3 different cover types are given.

		Cover type		
SPECIES	Riparian index	riparian	conifer	open land
Gray Catbird	.	4.9	.0	.0
Willow Flycatcher	110.56	19.4	.1	.3
Common Yellowthroat	109.29	19.2	.0	.6
Northern Waterthrush	55.37	13.6	.3	.0
Lincoln's Sparrow	55.07	5.8	.1	.2
Song Sparrow	35.93	36.5	.6	2.3
Yellow Warbler	28.48	29.0	.9	1.5
Red-eyed Vireo	27.15	10.5	.4	.3
American Redstart	22.41	14.9	.7	.5
Cedar Waxwing	16.62	7.6	.4	.8
Red-winged Blackbird	16.10	8.5	.0	2.3
Western Wood-Pewee	11.20	8.2	.5	1.5
Cordilleran Flycatcher	9.08	6.7	.9	.3
House Wren	6.71	8.5	1.0	2.0
Tree Swallow	5.72	8.0	.5	4.4
Lazuli Bunting	4.80	6.9	.8	3.5
Calliope Hummingbird	3.26	4.2	1.2	1.7
Black-headed Grosbeak	3.18	7.1	2.4	1.8
Ruffed Grouse	3.12	6.0	2.0	1.5
Dusky Flycatcher	3.04	32.5	9.6	14.3
Black-capped Chickadee	2.94	12.2	4.4	3.5
Red-naped Sapsucker	2.06	7.3	3.7	3.2

Table 3. Bird species relatively restricted to the conifer forest cover type, as indicated by a “conifer index” (see Methods). Under "Cover type", the percent occurrences of each species in the 3 different cover types are given.

		Cover type		
SPECIES	conifer index	conifer	open land	riparian
Evening Grosbeak	13.92	2.1	.2	1.3
White-breasted Nuthatch	8.29	1.3	.2	1.1
Red Crossbill	7.48	4.6	.6	.4
Hermit Thrush	6.52	6.0	.9	1.1
Golden-crowned Kinglet	6.30	18.4	2.9	8.5
Chestnut-backed Chickadee	5.85	3.6	.6	2.2
Common Raven	5.18	3.2	.6	2.2
Red-breasted Nuthatch	4.94	50.8	10.3	15.1
Williamson's Sapsucker	4.59	1.4	.3	.0
Hammond's Flycatcher	4.54	8.4	1.8	7.3
Townsend's Warbler	4.40	30.4	6.9	13.4
Pileated Woodpecker	3.90	3.6	.9	1.8
Brown Creeper	3.70	1.1	.3	.0
Ruby-crowned Kinglet	3.65	30.8	8.4	27.6
Mountain Chickadee	3.30	22.3	6.7	12.0
Solitary Vireo	3.14	18.3	5.8	8.7
Clark's Nutcracker	3.09	4.3	1.4	2.2
Yellow-rumped Warbler	2.93	50.4	17.2	26.3
Western Tanager	2.52	35.9	14.3	12.7
Pine Siskin	2.18	11.7	5.4	14.5
Gray Jay	2.14	7.5	3.5	2.4
Winter Wren	2.05	3.8	1.8	6.0
Varied Thrush	2.01	8.6	4.3	4.7
Townsend's Solitaire	1.67	12.6	7.5	5.8
Dark-eyed Junco	1.67	58.2	35.0	33.2
Swainson's Thrush	1.62	34.3	21.2	29.4
Cassin's Finch	1.57	3.4	2.1	2.4
Hairy Woodpecker	1.46	2.7	1.8	.9
Pine Grosbeak	1.42	1.1	.8	.2
Chipping Sparrow	1.26	32.5	25.9	26.5
Steller's Jay	1.25	2.5	2.0	1.3

Table 4. Bird species relatively restricted to open-land cover types, as indicated by a "conifer index" (see Methods). Under "Cover type", the percent occurrences of each species in the 3 different cover types are given.

		Cover type		
SPECIES	conifer index	conifer	open land	riparian
Savannah Sparrow	.00	.0	12.9	1.6
Brewer's Sparrow	.00	.0	7.5	.4
Brewer's Blackbird	.00	.0	3.5	1.8
Grasshopper Sparrow	.00	.0	6.7	.0
Horned Lark	.00	.0	6.1	.0
Western Meadowlark	.00	.1	31.3	6.7
Vesper Sparrow	.00	.2	37.6	4.7
Cliff Swallow	.01	.0	4.8	2.7
White-crowned Sparrow	.12	.4	3.4	1.3
Mountain Bluebird	.19	1.7	9.2	2.7

Table 5. Bird species that were not analyzed because they were not restricted to any of the three general cover types, and were not expected to be sensitive to fragmentation. Under "Cover type" are the percent occurrences of each species in the 3 different habitats.

			Cover type		
SPECIES	conifer index	riparian index	conifer	open land	riparian
Nashville Warbler	2.44	2.23	1.5	.6	2.9
Wilson's Warbler	1.04	.91	2.2	2.1	2.0
Red-tailed Hawk	.99	.73	.9	.9	.7
American Robin	.94	2.39	20.9	22.2	50.8
Northern Flicker	.87	1.34	8.7	10.0	12.0
Brown-headed Cowbird	.84	2.24	7.8	9.4	18.3
Orange-crowned Warbler	.81	1.20	9.7	12.0	12.2
MacGillivray's Warbler	.81	2.04	19.8	24.5	42.5
Warbling Vireo	.71	2.12	14.8	20.9	34.3
Fox Sparrow	.68	1.40	2.7	4.0	4.2
Olive-sided Flycatcher	.66	.77	3.4	5.1	2.9
Rufous Hummingbird	.55	1.03	1.3	2.3	1.6
Rufous-sided Towhee	.39	2.87	1.1	2.8	4.2

Table 6. Correlation coefficients between the three landscape variables in each of the three habitat groupings.

	Patch Size	Edge Density
Conifer points (n=3769):		
Percent conifer	.69	-.48
Edge Density -.42	-	
Riparian points (n=1706):		
Percent riparian	.24	.51
Edge Density .11	-	
Open points (n=525):		
Percent open	.90	-.32
Edge Density -.40	-	

Table 7. Results of logistic regression analysis used to describe the relationship between each of the three landscape variables and the frequency of occurrence of bird species characteristic of conifer forests. "No. hits" is the number of points out of 3769 at which the species was detected. The sign of the regression coefficient, chi-square statistic, and p-value indicating the level of significance are included for each landscape variable. The species are ordered by their relationship to the percent conifer variable, from the strongest positive to the strongest negative association.

		Percent conifer land				Patch size			Edge density		
Species	No. hits	sign	statistic	p		sign	statistic	p	sign	statistic	p
Townsend's Warbler	1221		52.7	.00			29.1	.00	-	12.6	.00
Varied Thrush	403		40.8	.00			18.9	.00	-	16.1	.00
Golden-crowned Kinglet	841		24.8	.00			23.3	.00	-	16.4	.00
Chestnut-backed Chickadee	167		22.6	.00			.9	.33	-	42.1	.00
Winter Wren	333		15.8	.00			6.3	.01	-	6.3	.01
Red-breasted Nuthatch	1647		9.5	.00			10.3	.00	-	19.1	.00
Swainson's Thrush	1255		5.2	.02			2.9	.09	-	4.2	.04
Pileated Woodpecker	129		2.2	.14			1.9	.17	-	.1	.71
Pine Grosbeak	35		1.8	.18			8.2	.00		.7	.40
Gray Jay	279		.4	.53			3.1	.08		.7	.39
Steller's Jay	109		.3	.57			.5	.50	-	2.5	.11
Solitary Vireo	568		.2	.70			.1	.70		.8	.38
Yellow-rumped Warbler	1728		.2	.65			.1	.73		.6	.45
Hermit Thrush	200		.2	.68			3.1	.08		2.1	.14
Hairy Woodpecker	125		.0	.85			.1	.75		.2	.11
Evening Grosbeak	59	-	.2	.65		-	2.5	.17		1.7	.20
Brown Creeper	50	-	.3	.58		-	.3	.56	-	2.5	.12
Hammond's Flycatcher	424	-	.6	.44		-	7.3	.01	-	.5	.48
White-breasted Nuthatch	42	-	.8	.37		-	2.5	.12		.3	.59
Townsend's Solitaire	404	-	.9	.34		-	.6	.44		3.0	.08
Williamson's Sapsucker	42	-	1.6	.20		-	.8	.37		2.3	.13
Red Crossbill	136	-	2.4	.12		-	4.5	.03		5.2	.02
Western Tanager	1133	-	3.7	.05		-	5.9	.02		2.5	.12
Common Raven	104	-	4.7	.03		-	2.7	.10		3.5	.06
Clark's Nutcracker	129	-	9.7	.00		-	2.3	.13		13.7	.00
Cassin's Finch	120	-	12.2	.00		-	14.6	.00		19.8	.00
Chipping Sparrow	1062	-	15.8	.00		-	27.9	.00		24.6	.00
Dark-eyed Junco	2073	-	19.1	.00		-	2.6	.11		1.9	.17
Ruby-crowned Kinglet	1040	-	22.8	.00		-	11.1	.00		46.0	.00
Mountain Chickadee	786	-	25.6	.00		-	11.1	.00		8.8	.00
Pine Siskin	446	-	28.6	.00		-	16.7	.00		13.4	.00

Table 8. Results of logistic regression analysis used to describe the relationship between each of the three landscape variables and the frequency of occurrence of bird species characteristic of riparian lands. "No. hits" is the number of points out of 3769 at which the species was detected. The sign of the regression coefficient, chi-square statistic, and p-value indicating the level of significance are included for each landscape variable. The species are ordered by their relationship to the percent riparian variable, from the strongest positive to the strongest negative association.

		Percent riparian land				Patch size			Edge density		
Species	No. hits	sign	statistic	p		sign	statistic	p	sign	statistic	p
Western Wood-Pewee	20		21.4	.00			.3	.56		14.6	.00
American Redstart	27		9.5	.00			.8	.36		1.8	.18
Cedar Waxwing	12		8.2	.00			.2	.65		6.1	.01
Red-naped Sapsucker	26		6.7	.01			.1	.80		.7	.40
House Wren	33		5.5	.02		-	.1	.71		1.3	.26
Yellow Warbler	59		4.9	.03		-	2.1	.14		9.4	.00
Dusky Flycatcher	124		2.9	.09			.4	.53		5.5	.02
Tree Swallow	10		2.9	.09			.0	.95		2.4	.12
Black-headed Grosbeak	16		2.7	.10			.1	.80		.7	.39
Song Sparrow	89		2.3	.13			.0	.98		6.0	.01
Willow Flycatcher	36		2.2	.14		-	1.0	.33		1.0	.32
Ruffed Grouse	26		1.6	.21		-	.2	.65		.4	.52
Calliope Hummingbird	11		.7	.39		-	.4	.53		.0	.94
Red-eyed Vireo	12		.5	.48		-	.9	.34		.4	.51
Northern Waterthrush	22		.4	.53		-	.2	.68	-	.4	.53
Red-winged Blackbird	9		.1	.71			.5	.49		.5	.49
Lazuli Bunting	20		.1	.71			.0	.99		.4	.53
Gray Catbird	11		.1	.74		-	.9	.34		.8	.36
Cordilleran Flycatcher	24		.1	.78		-	.0	.83	-	1.0	.32
Common Yellowthroat	27		.1	.79			.1	.73		.4	.52
Lincoln's Sparrow	14	-	.1	.78		-	1.6	.21		1.4	.23
Black-capped Chickadee	27	-	.3	.60		-	.6	.45		.0	.99

Table 9. Results of logistic regression analysis used to describe the relationship between each of the three landscape variables and the frequency of occurrence of bird species characteristic of open lands. "No. hits" is the number of points out of 3769 at which the species was detected. The sign of the regression coefficient, chi-square statistic, and p-value indicating the level of significance are included for each landscape variable. The species are ordered by their relationship to the percent open-land variable, from the strongest positive to the strongest negative association.

		Percent open land				Patch size			Edge density		
Species	No. hits	sign	statistic	p		sign	statistic	p	sign	statistic	p
Western Meadowlark	320		762.0	.00			732.2	.00	-	201.6	.00
Vesper Sparrow	413		515.7	.00			444.1	.00	-	135.9	.00
Savannah Sparrow	130		206.0	.00			192.1	.00	-	10.7	.00
Horned Lark	47		118.0	.00			108.1	.00	-	64.1	.00
Grasshopper Sparrow	51		107.5	.00			106.5	.00	-	69.3	.00
Brewer's Sparrow	87		71.2	.00			56.1	.00	-	16.7	.00
Brewer's Blackbird	53		61.7	.00			56.9	.00	-	13.0	.00
Cliff Swallow	47		47.1	.00			47.1	.00		10.9	.00
Mountain Bluebird	150		20.8	.00			30.5	.00	-	5.7	.02
White-crowned Sparrow	85		.0	.91			.1	.75		7.2	.01

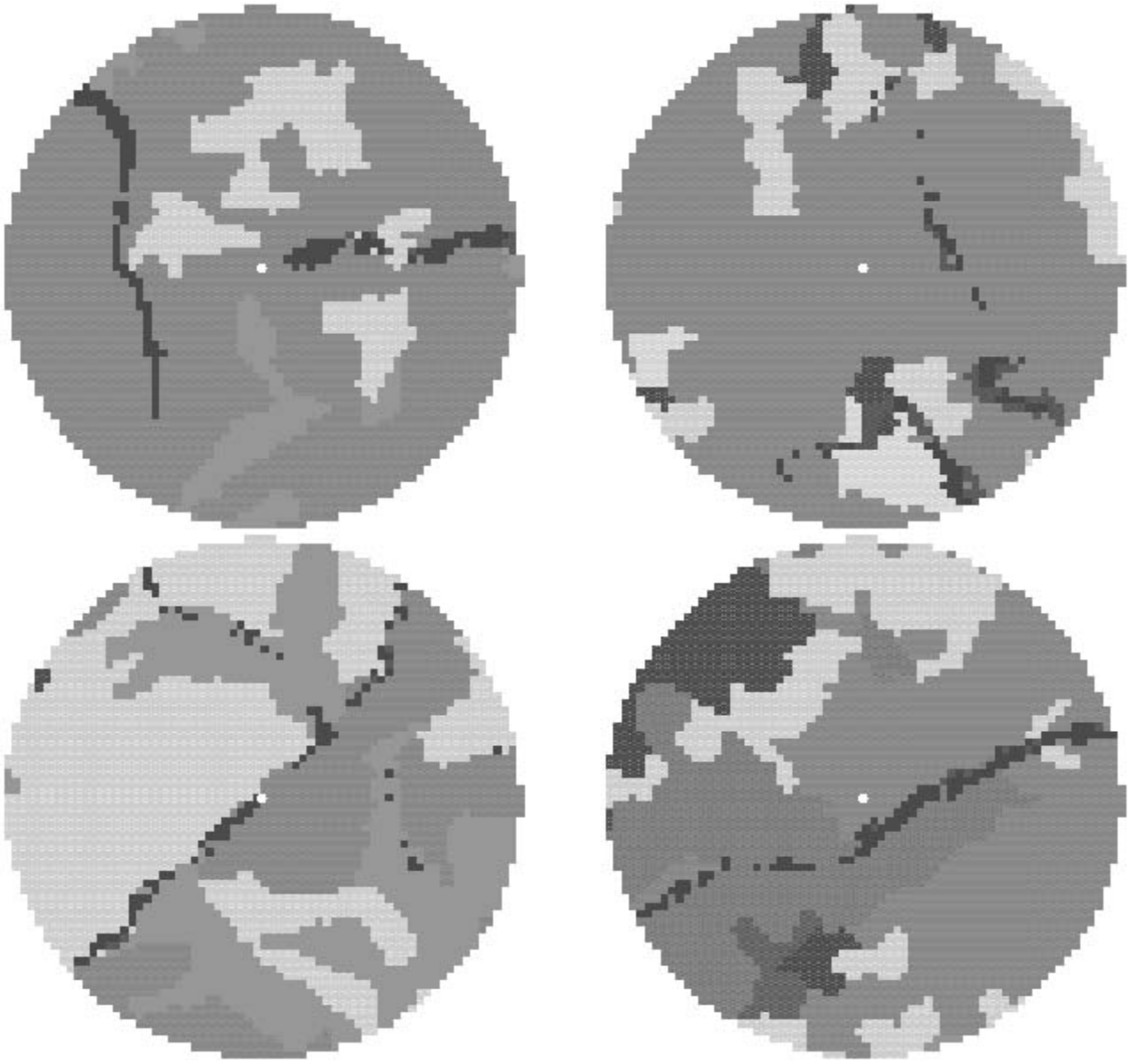


Figure 1. Four examples of 1-km-radius landscapes created from the GIS database, using the 15 cover types listed in Table 1. The lighter colors are open areas; the dark strings of patches are riparian areas; and the medium-gray areas are conifer forests of various types.

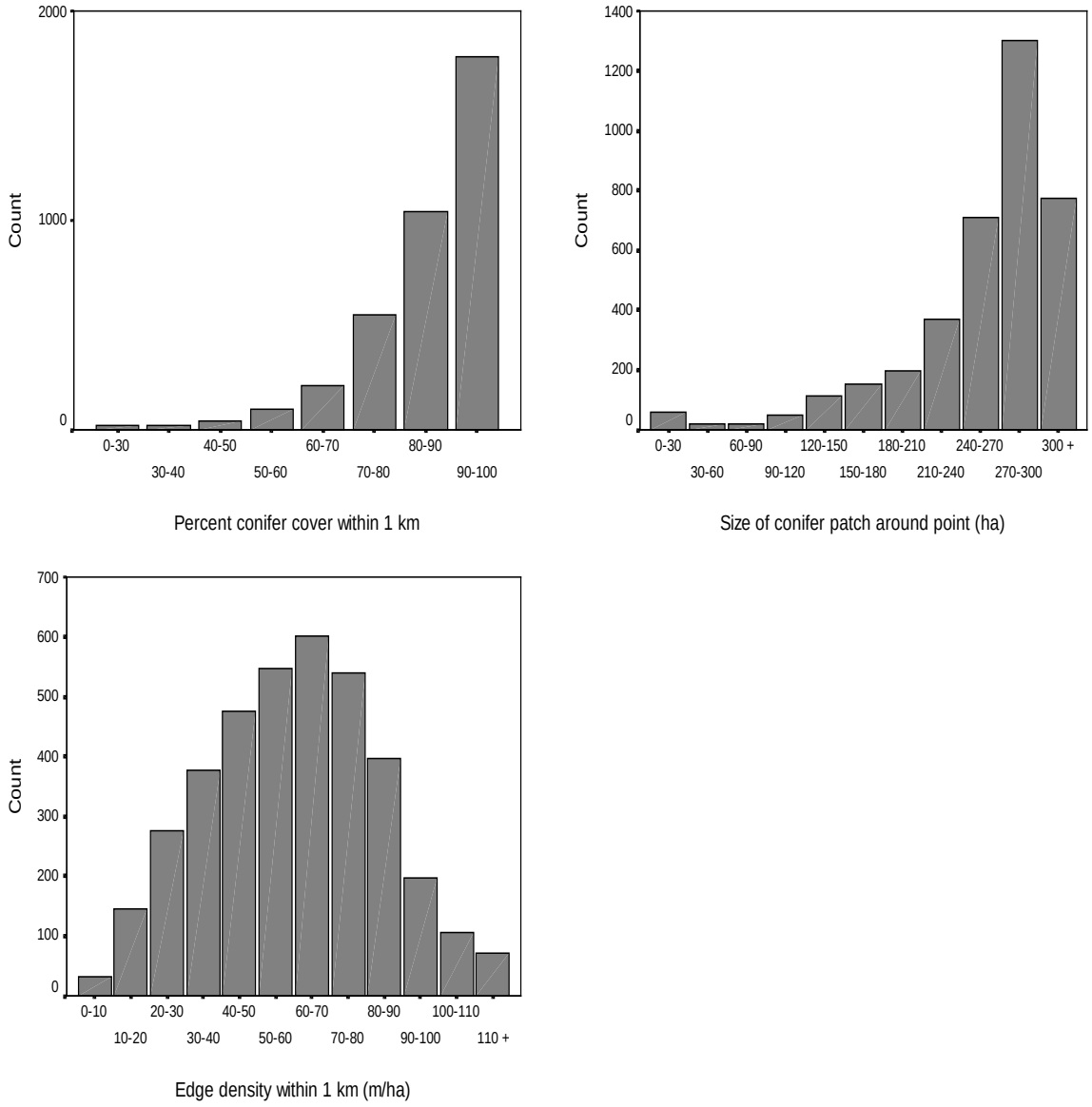


Figure 2. Distribution of sample sizes for landscape variable categories used in analyses of conifer-restricted bird species (Figures 5-11).

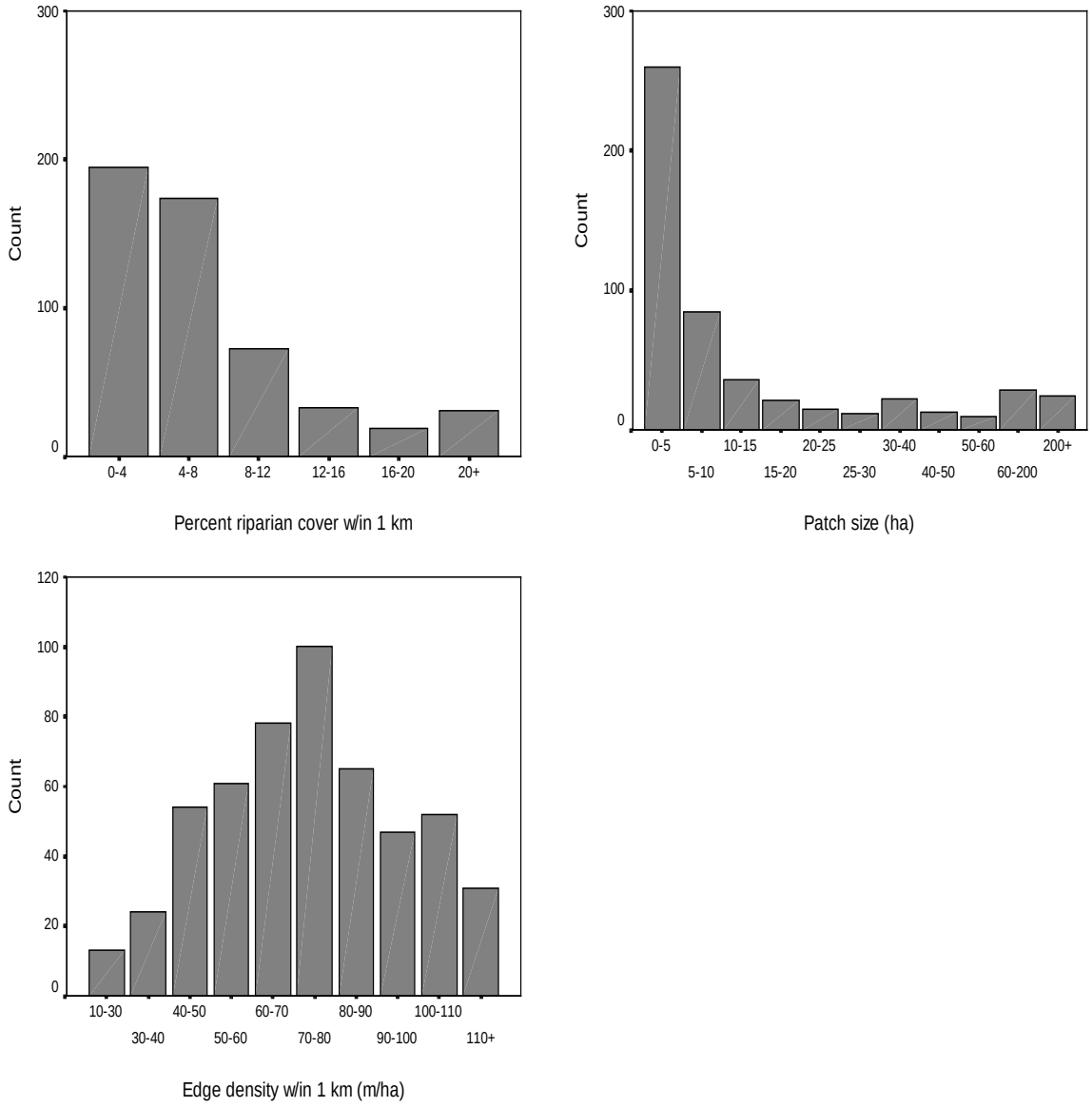


Figure 3. Distribution of sample sizes for landscape variable categories used in analyses of riparian-restricted bird species (Figures 12-17).

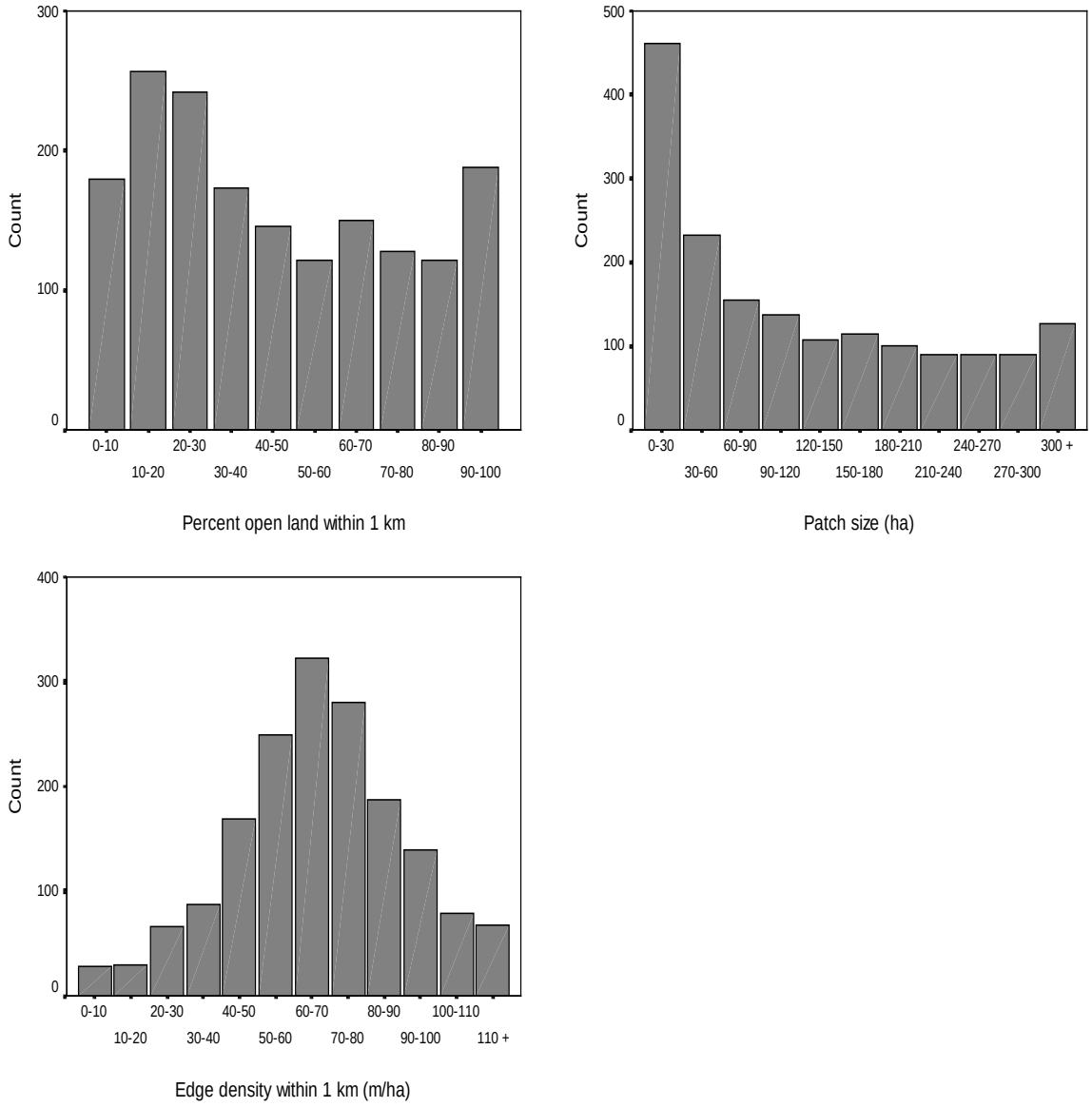


Figure 4. Distribution of sample sizes for landscape variable categories used in analyses of bird species restricted to open lands (Figures 18-24).

Townsend's Warbler

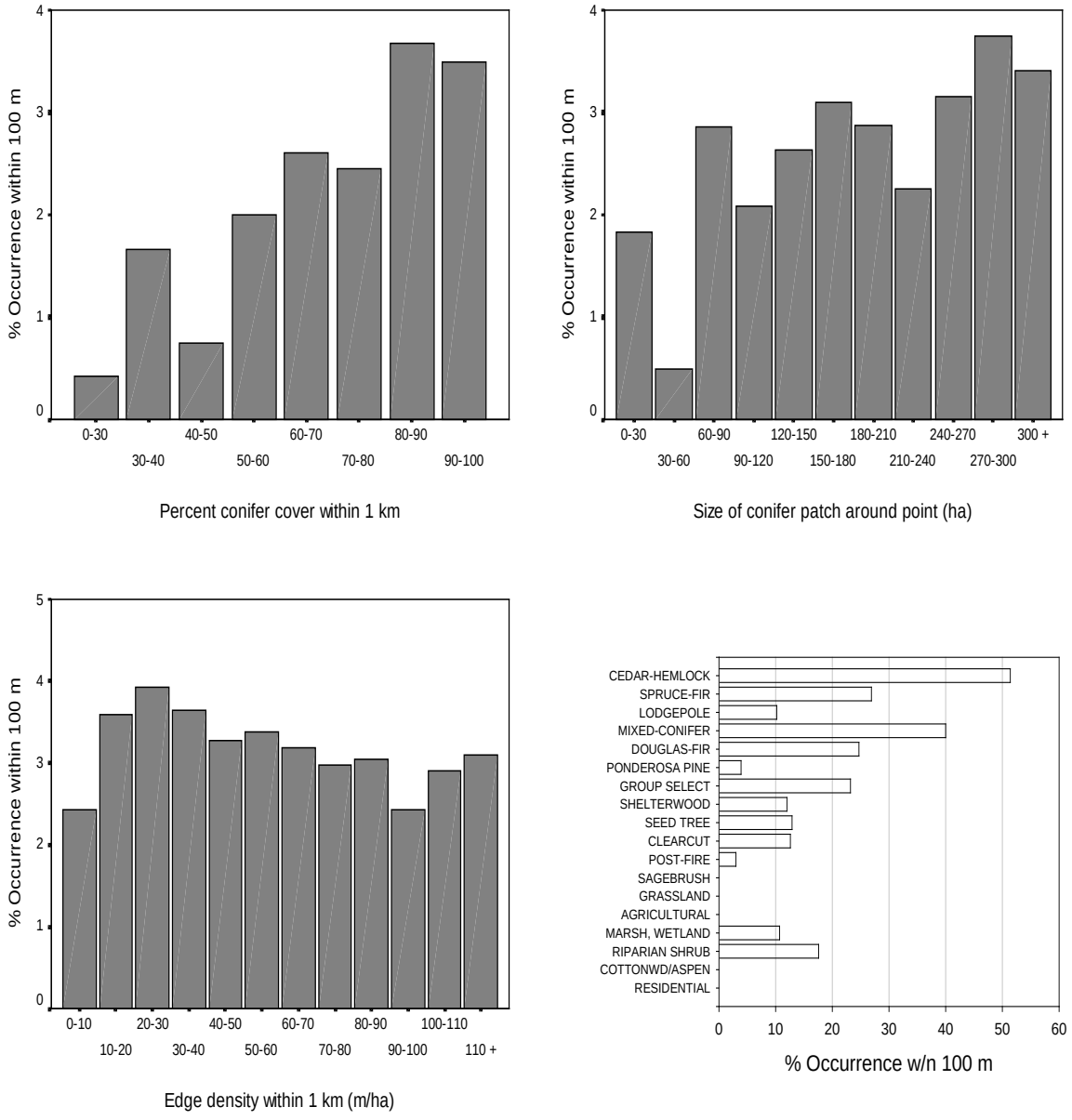


Figure 5. Townsend's Warbler showed a strong response to all three landscape variables, especially to the percent of conifer lands in the landscape circle (it had the strongest association of any species for this variable). The other two variables did not explain any additional information after percent conifer was controlled for, even though they were both highly significant in the univariate case ($p < .001$). The fourth graph is the previously reported (Hutto 1997) habitat distribution model.

Varied Thrush

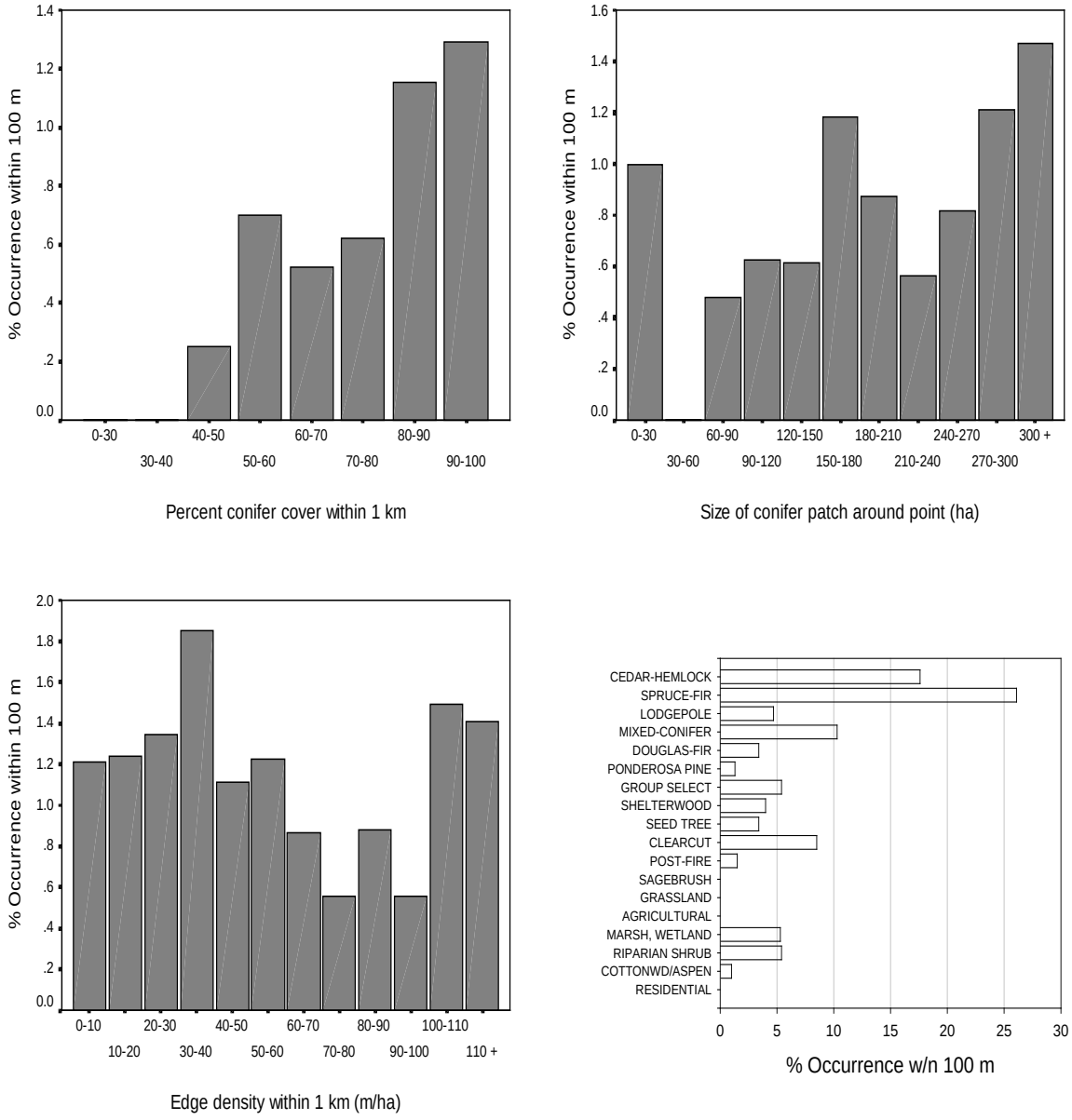


Figure 6. Varied Thrush showed a strong response to all three landscape variables, especially to the percent of conifer lands in the landscape circle. The other two variables did not explain any additional information after percent conifer was controlled for, even though they were both highly significant in the univariate case ($p < .001$). The fourth graph is the previously reported (Hutto 1997) habitat distribution model.

Golden-crowned Kinglet

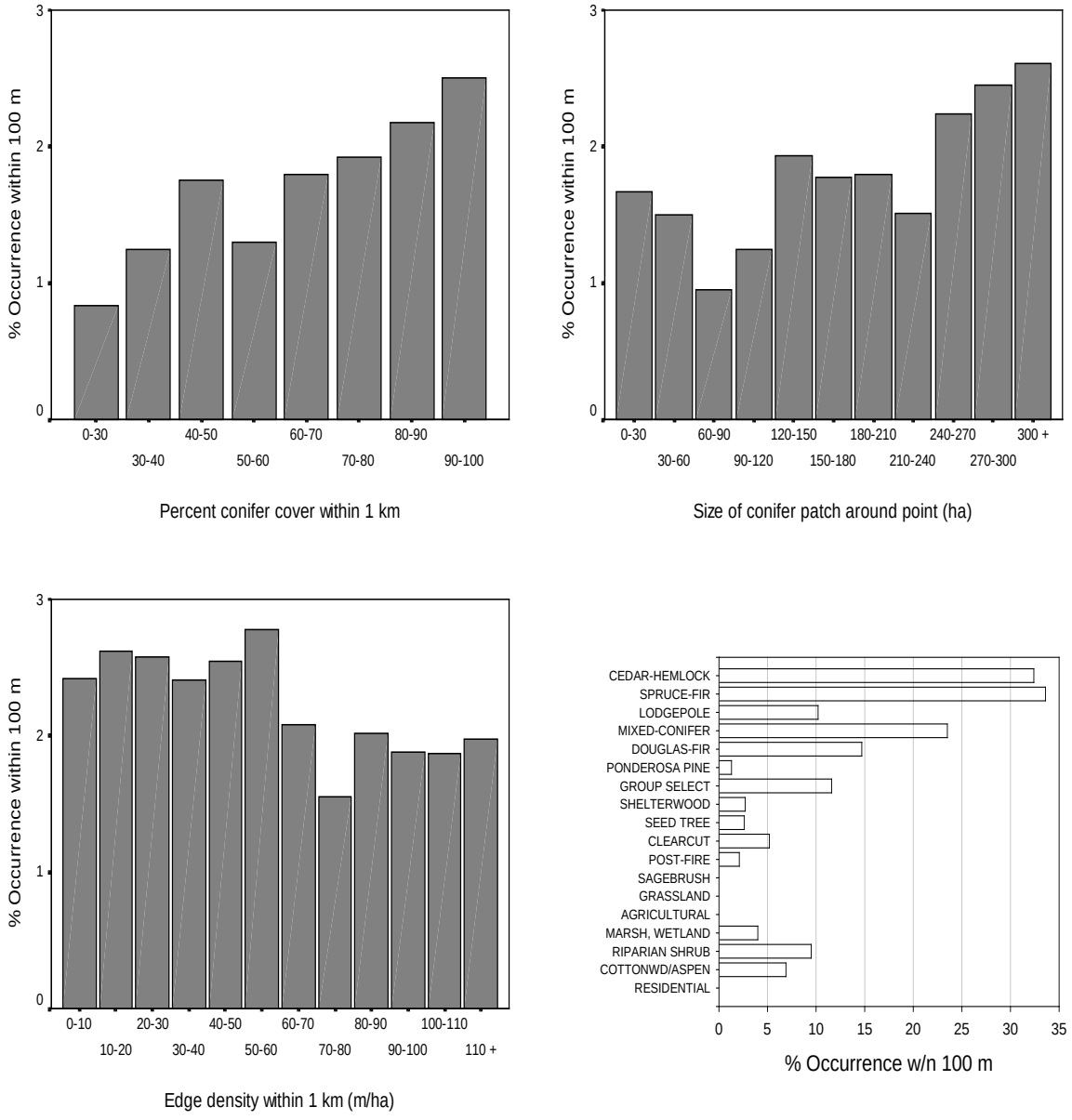


Figure 7. Golden-crowned Kinglet showed a strong response to all three landscape variables, especially to the percent of conifer lands in the landscape circle. The other two variables did not explain any additional information after percent conifer was controlled for, even though they were both highly significant in the univariate case ($p < .001$). The fourth graph is the previously reported (Hutto 1997) habitat distribution model.

Chestnut-backed Chickadee

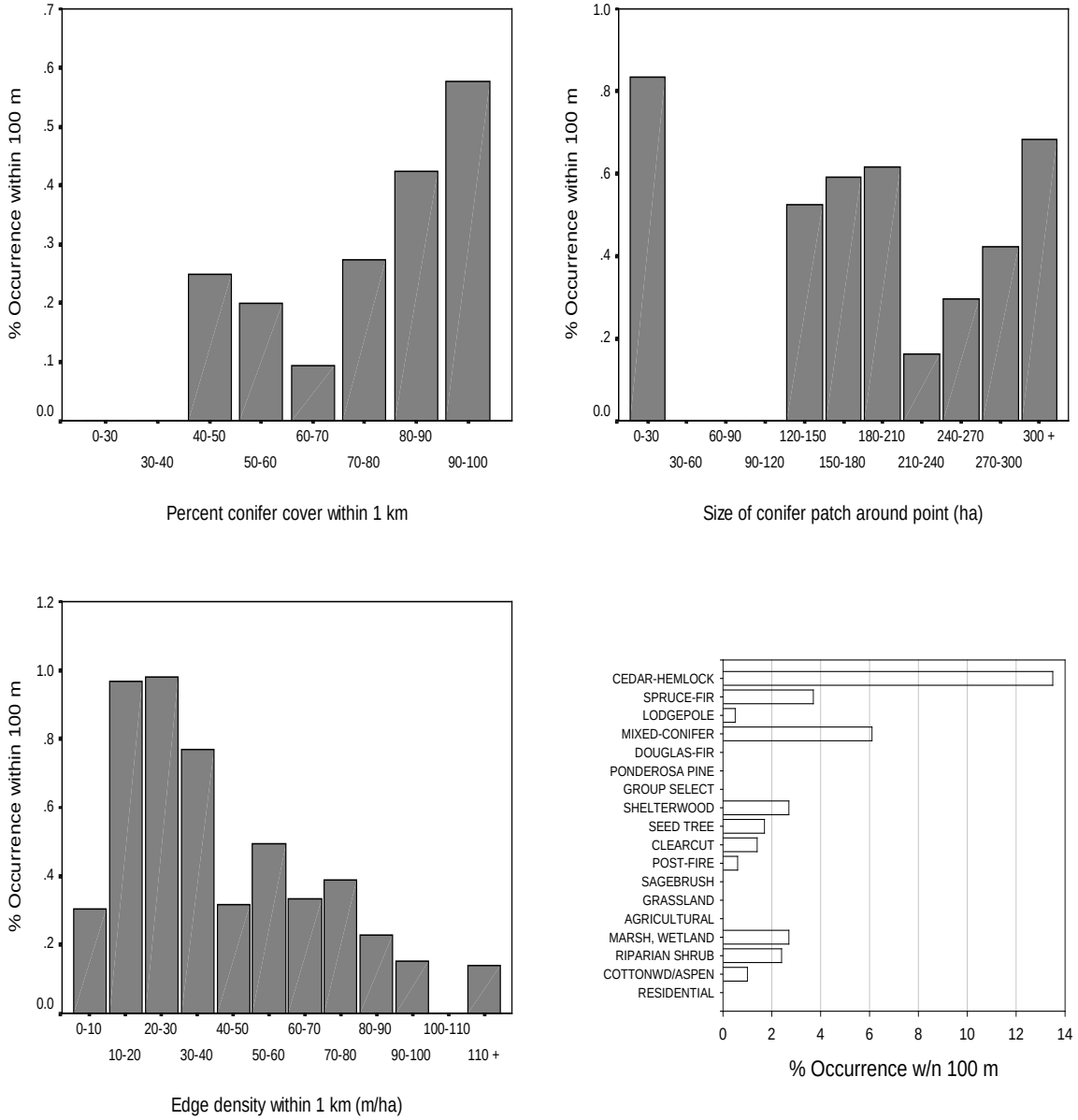


Figure 8. Like the other "landscape-sensitive" species, the Chestnut-backed Chickadee showed a strong positive response to the percent of conifer cover in the landscape, and a negative response to edge density. It was not associated with patch size, however, although in a forward stepwise procedure, all 3 variables were entered into a multivariate model. The fourth graph is the previously reported (Hutto 1997) habitat distribution model.

Winter Wren

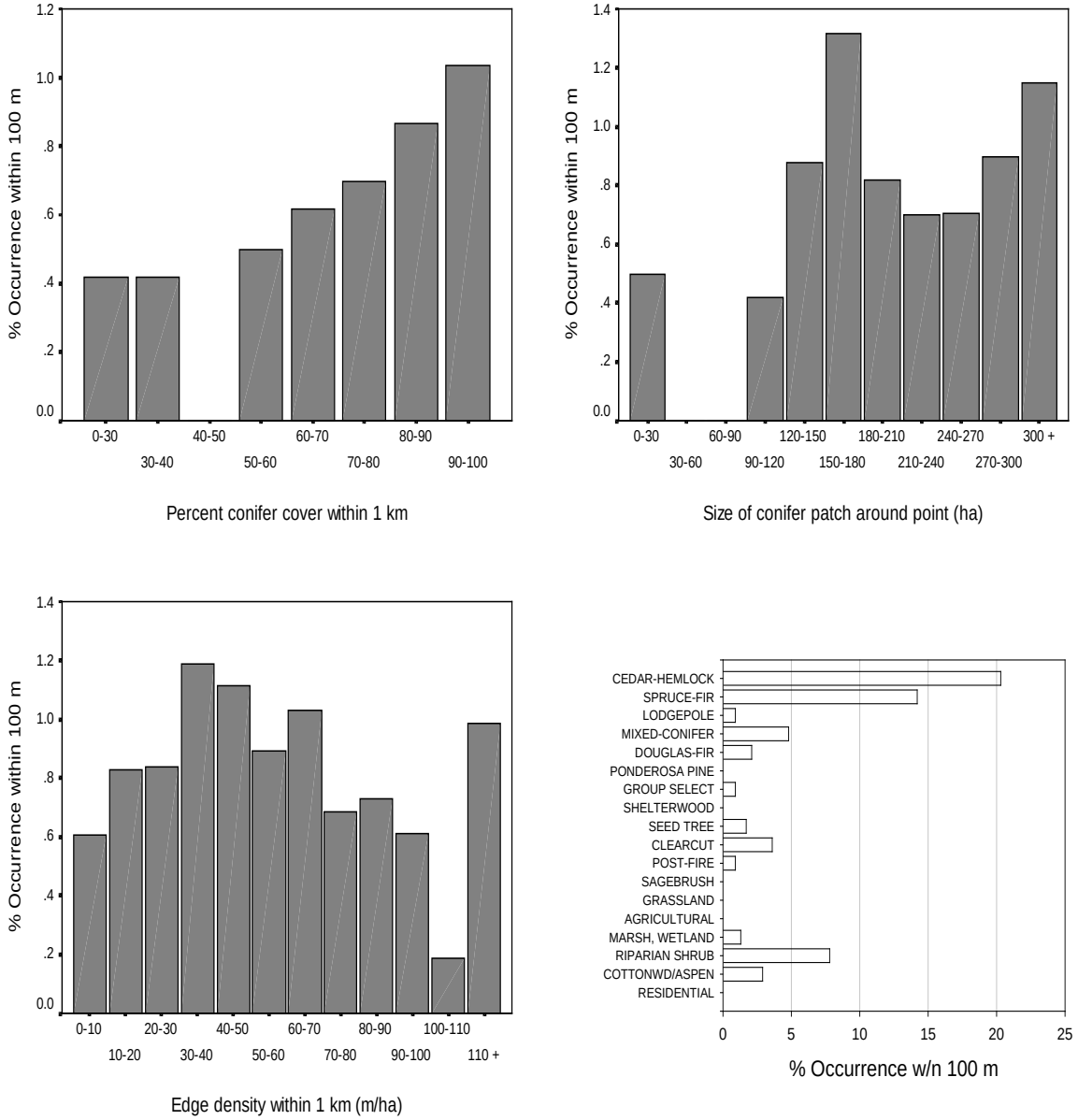


Figure 9. Although the Winter Wren could be considered a riparian species, the streamsides where it occurs are usually within mesic conifer habitats (especially cedar-hemlock). It is apparently sensitive to the extent of this habitat, as this species showed a strong response to all three landscape variables, especially to the percent of conifer lands in the landscape circle. The other two variables did not explain any additional information after percent conifer was controlled for, even though they were both significant in the univariate case ($p = .012$). The fourth graph is the previously reported (Hutto 1997) habitat distribution model.

Red-breasted Nuthatch

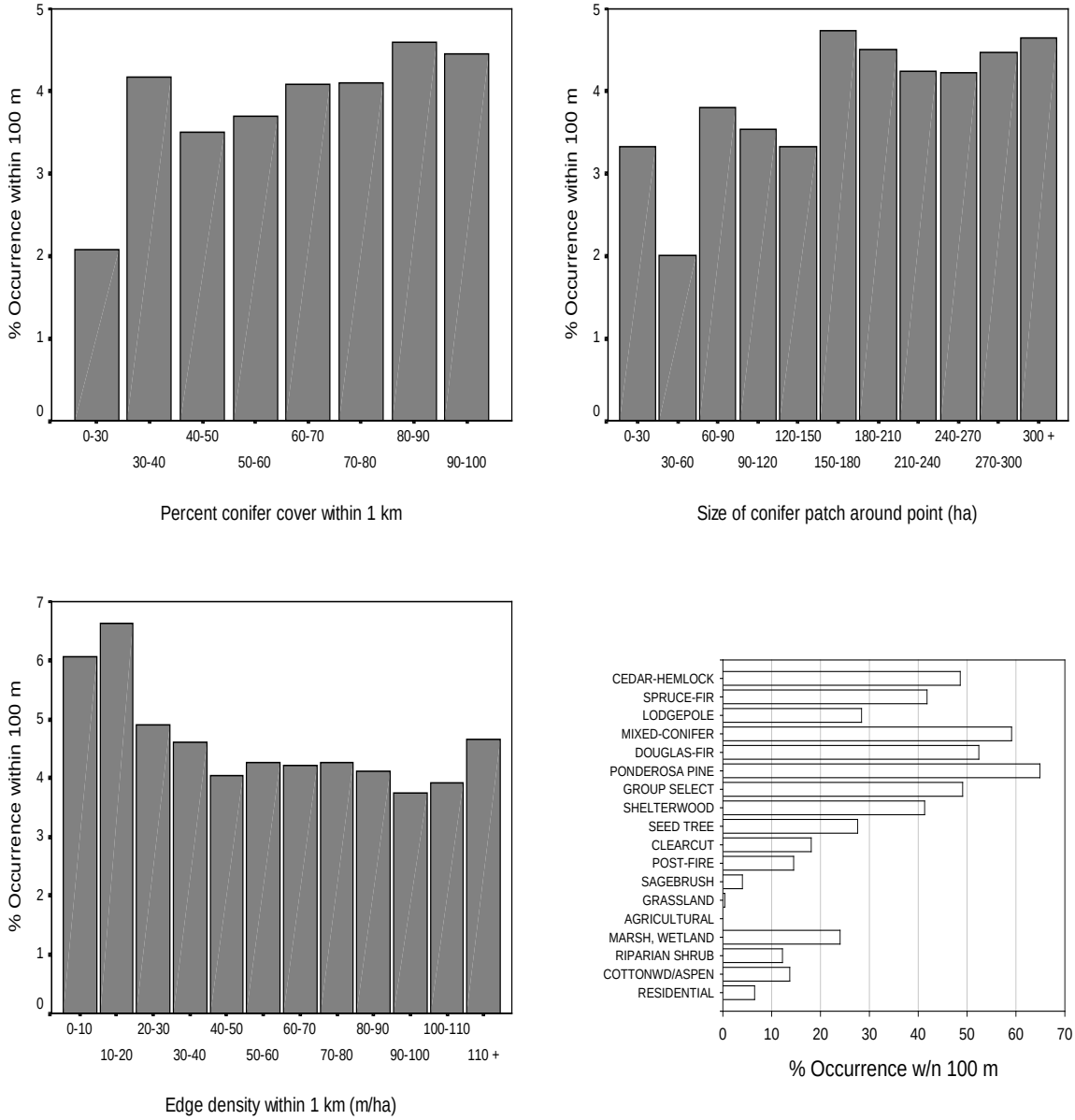


Figure 10. The Red-breasted Nuthatch showed a strong response to all three landscape variables, especially to the percent of conifer lands in the landscape circle. This species differed from the other potentially "landscape-sensitive" species, in that the negative response to edge density was the strongest of the three associations with the landscape variables. Although this species occured in a wider range of cover types than the other "landscape-sensitive" species, it apparently is still sensitive to fragmentation of the conifer landscape. The fourth graph is the previously reported (Hutto 1997) habitat distribution model.

Swainson's Thrush

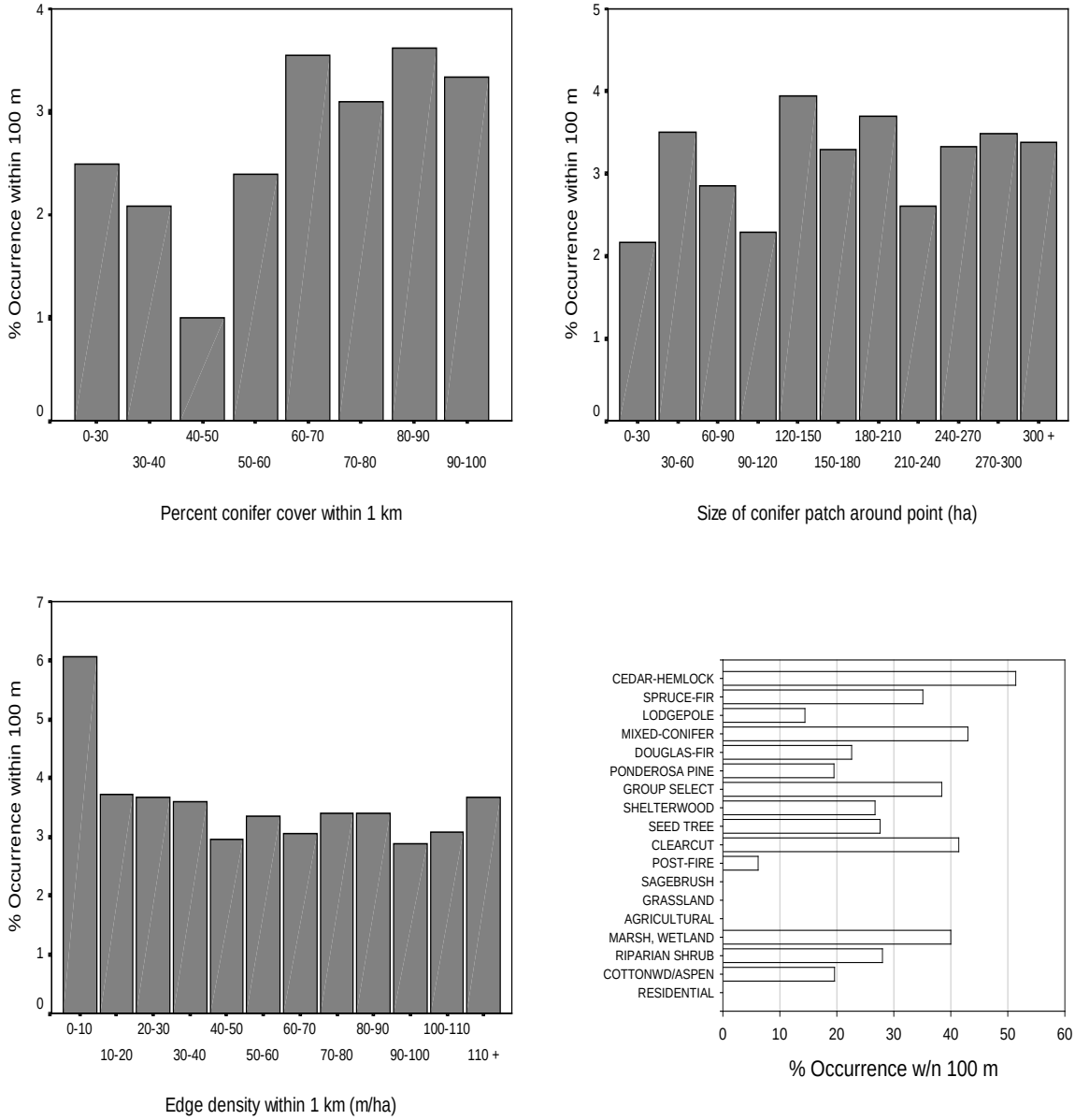


Figure 11. Like the other "landscape-sensitive" species, the Swainson's Thrush showed a strong positive response to the percent of conifer cover in the landscape, and a negative response to edge density. It was not associated with patch size, however, although there was a strong positive trend (p=.09). Edge density did not explain any additional information after controlling for percent conifer. The fourth graph is the previously reported (Hutto 1997) habitat distribution model.

Western Wood-Pewee

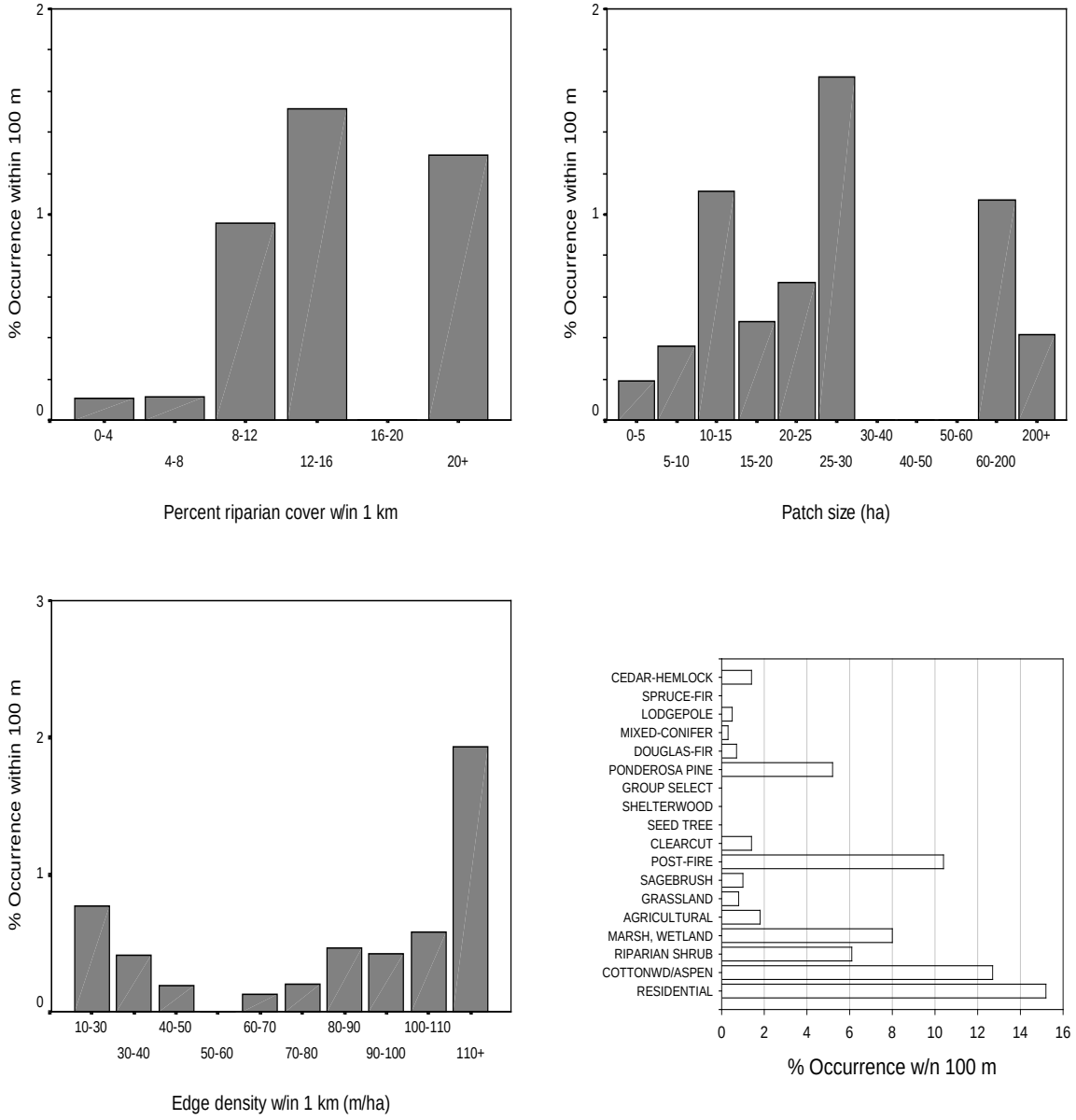


Figure 12. The Western Wood-Pewee had the strongest associations with landscape variables of any riparian species (the positive responses to percent riparian cover and edge density were both highly significant; $p < .0001$). Edge density did not explain any additional information after controlling for percent riparian. The fourth graph is the previously reported (Hutto 1997) habitat distribution model.

American Redstart

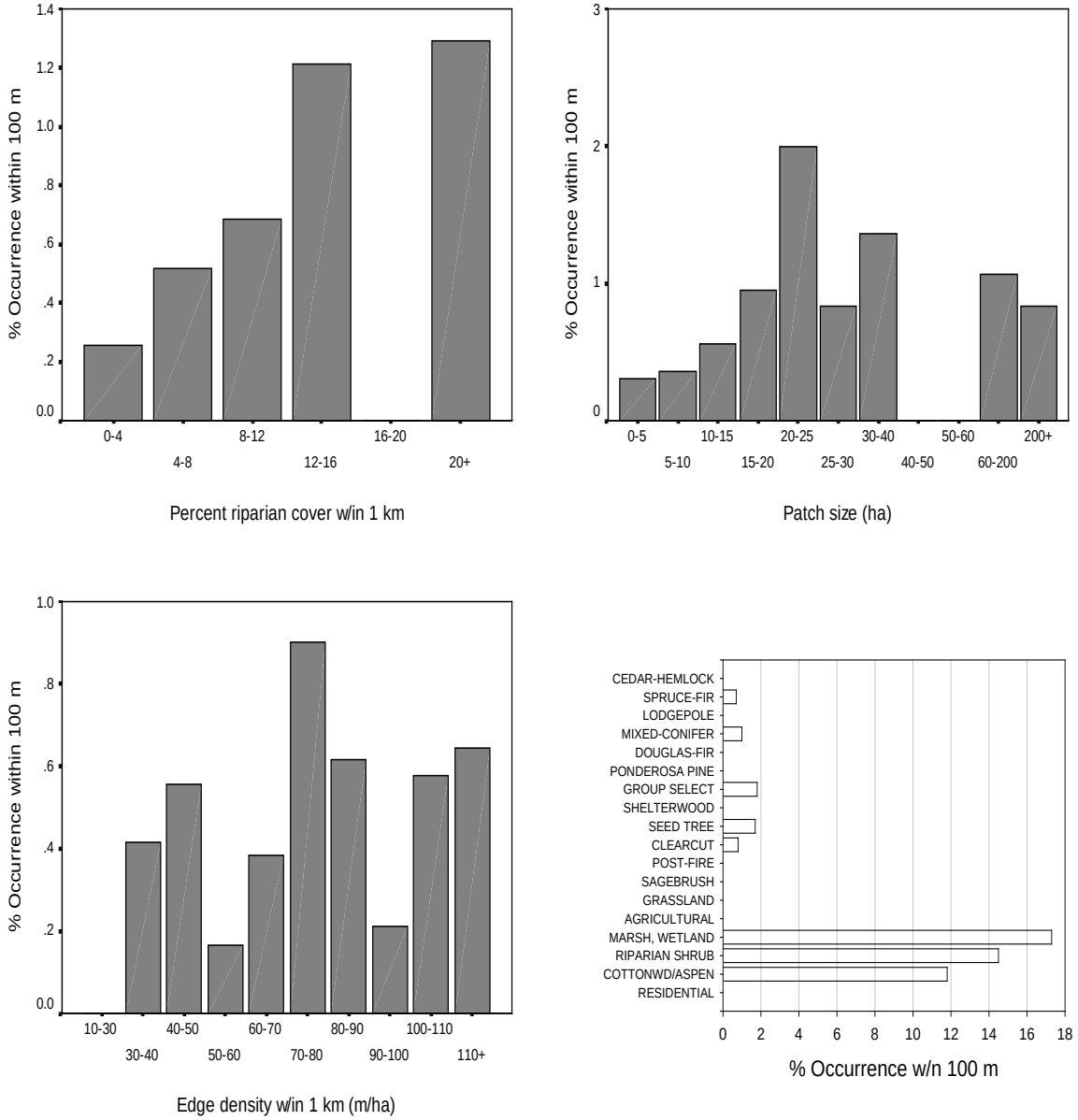


Figure 13. The presence of American Redstart was significantly positively associated with percent riparian cover within 1 km, but was not associated with the other landscape variables.

Cedar Waxwing

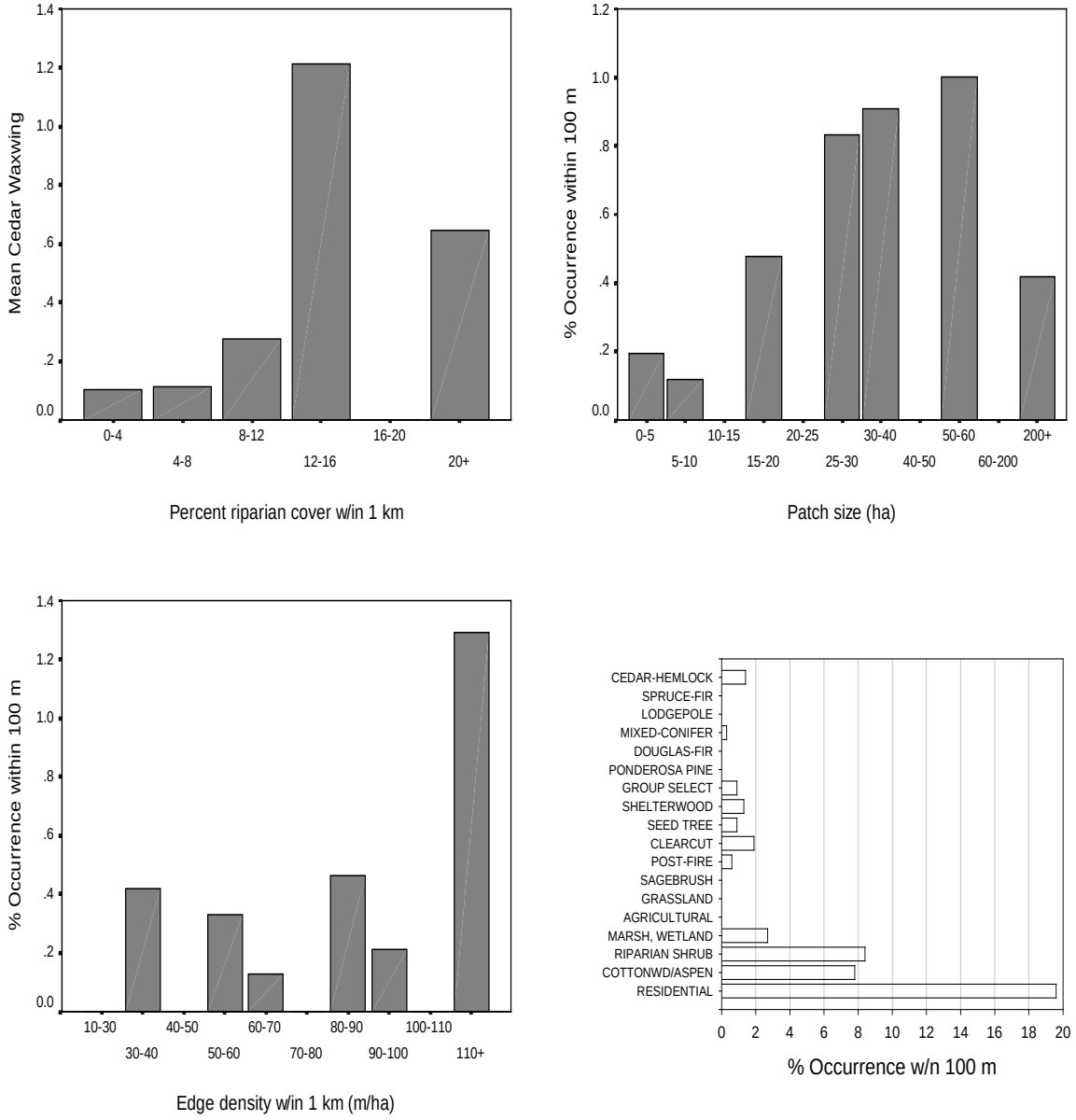


Figure 14. The presence of Cedar Waxwing was positively associated with percent riparian cover within 1 km and also positively associated with edge density.

Red-naped Sapsucker

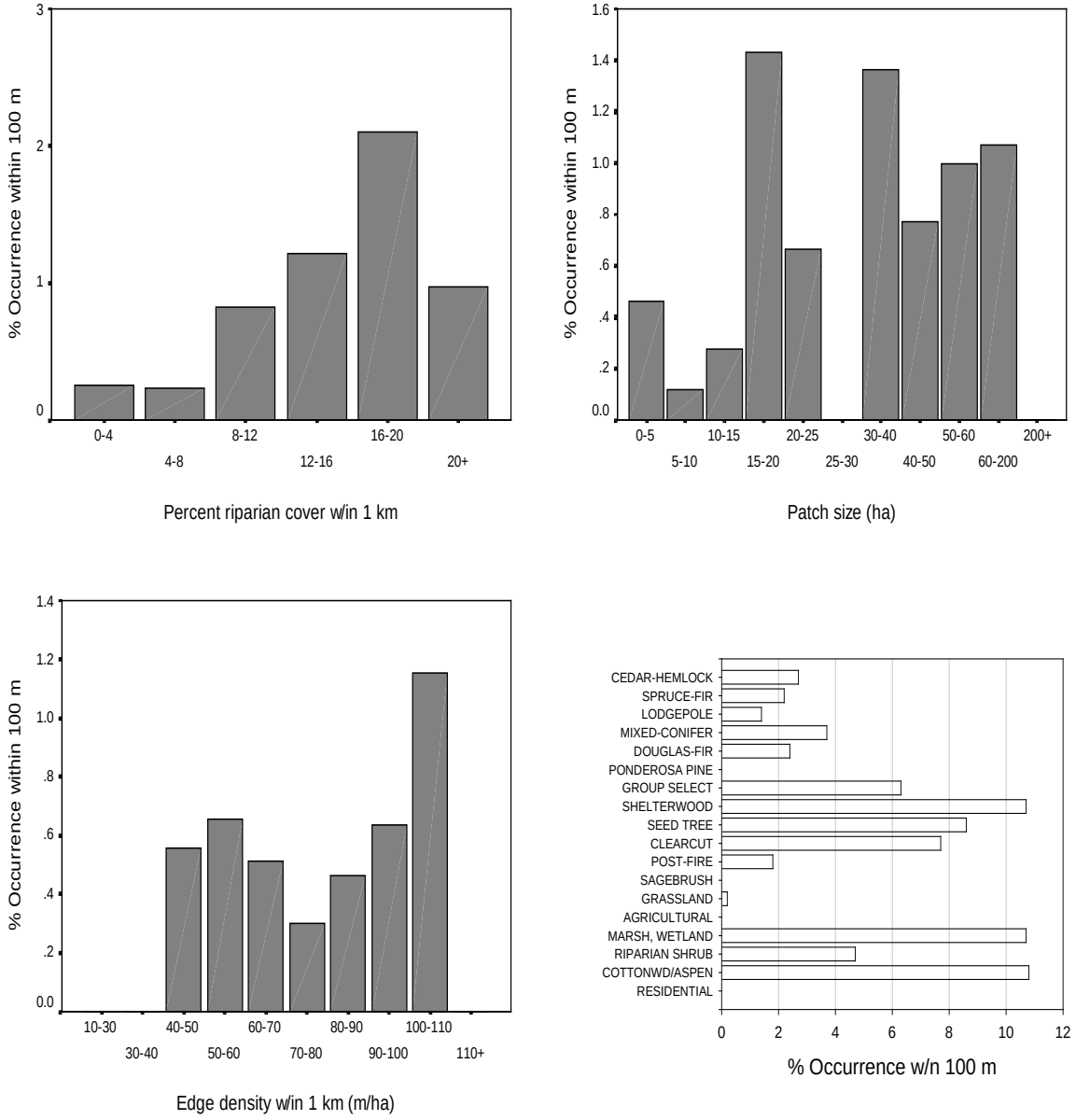


Figure 15. The presence of Red-naped Sapsucker was positively associated with percent riparian cover within 1 km, but not with the other two landscape variables.

House Wren

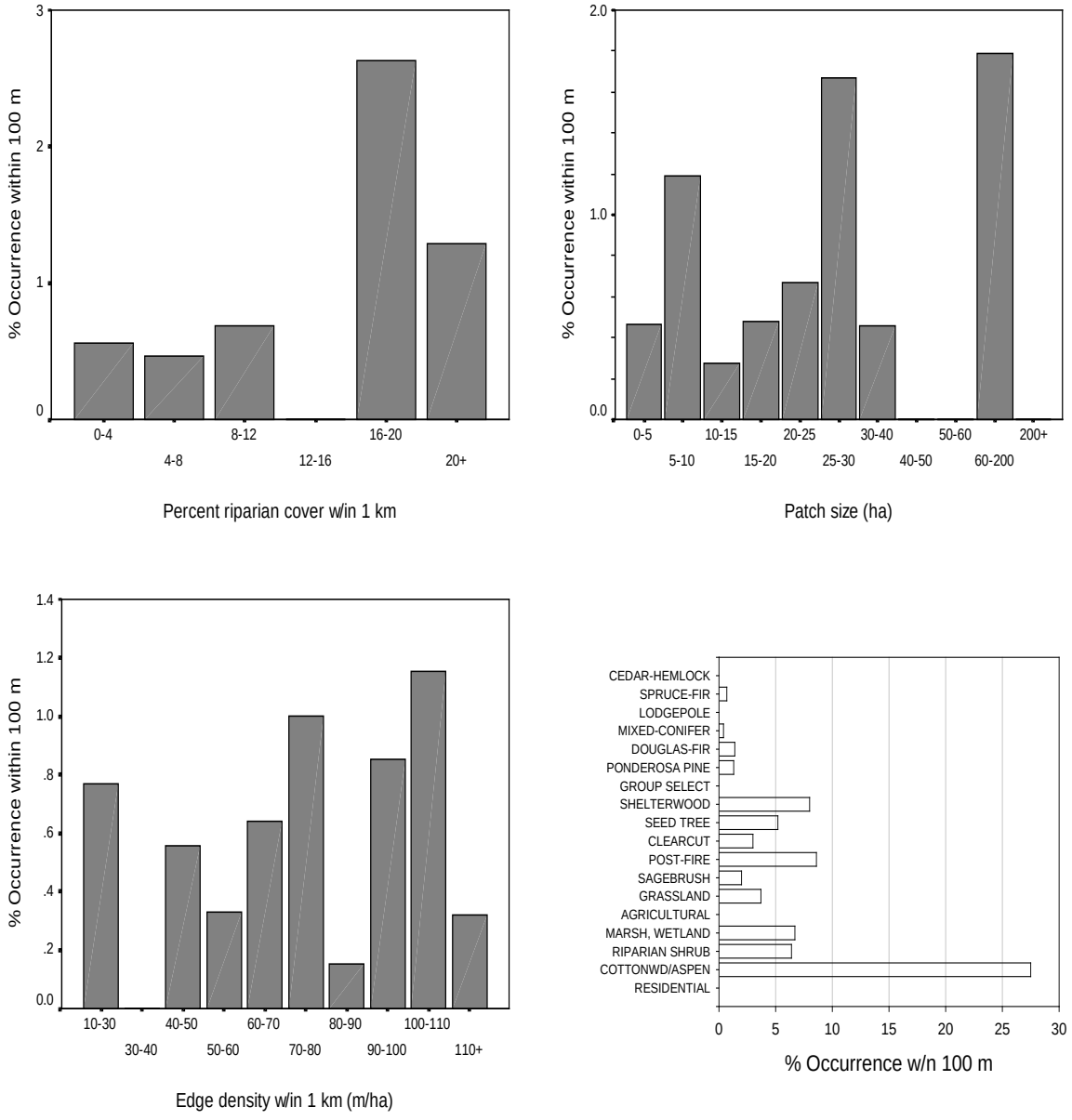


Figure 16. The presence of House Wren was positively associated with percent riparian cover within 1 km, but not with the other two landscape variables.

Yellow Warbler

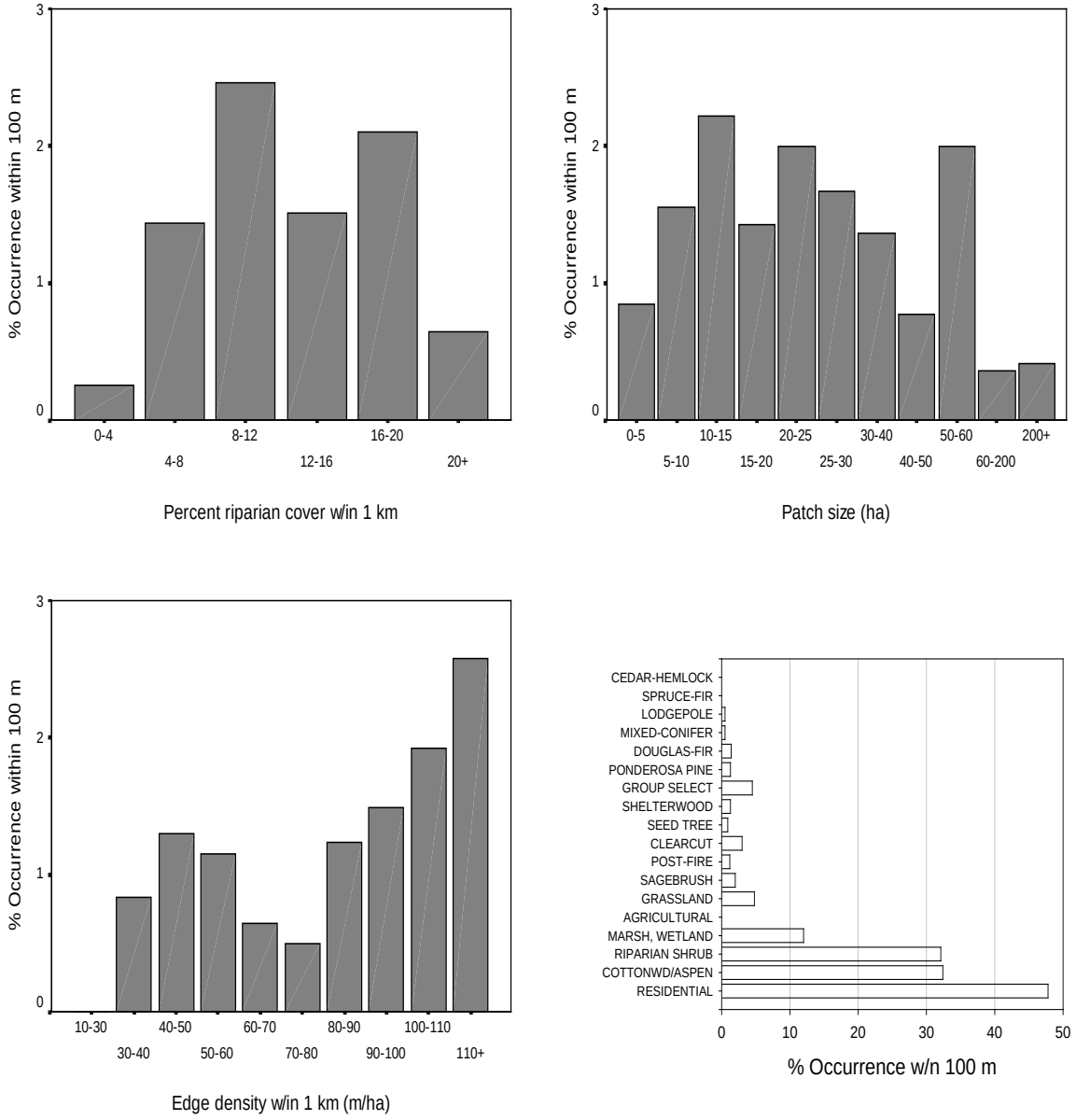


Figure 17. The presence of Yellow Warbler was positively associated with percent riparian cover within 1 km and also positively associated with edge density.

Western Meadowlark

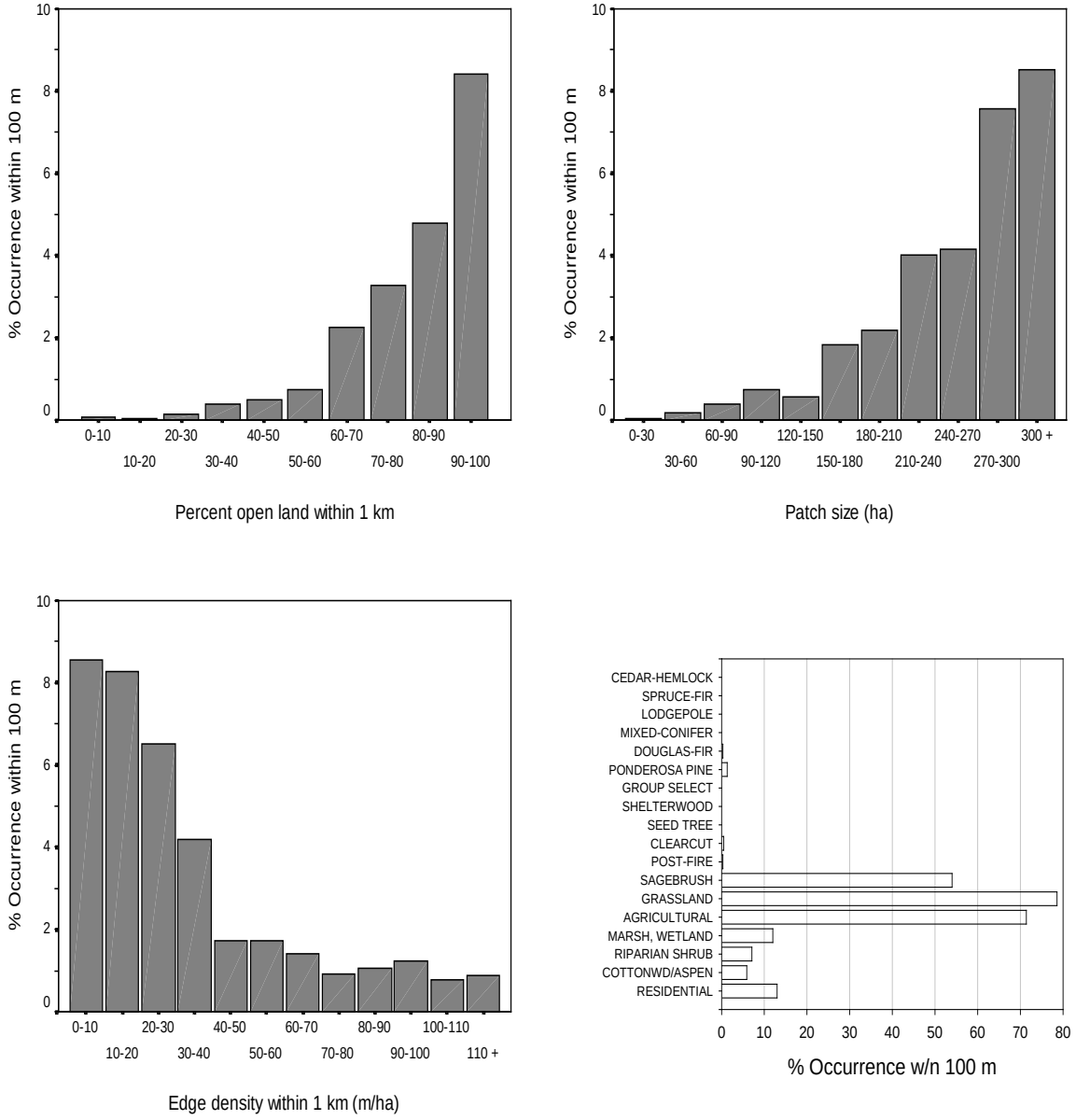


Figure 18. The presence of Western Meadowlark was significantly associated with all three landscape variables, but some of the associateion is certainly an artifact of using open shrubland points in the analysis, as explained more fully in the discussion.

Vesper Sparrow

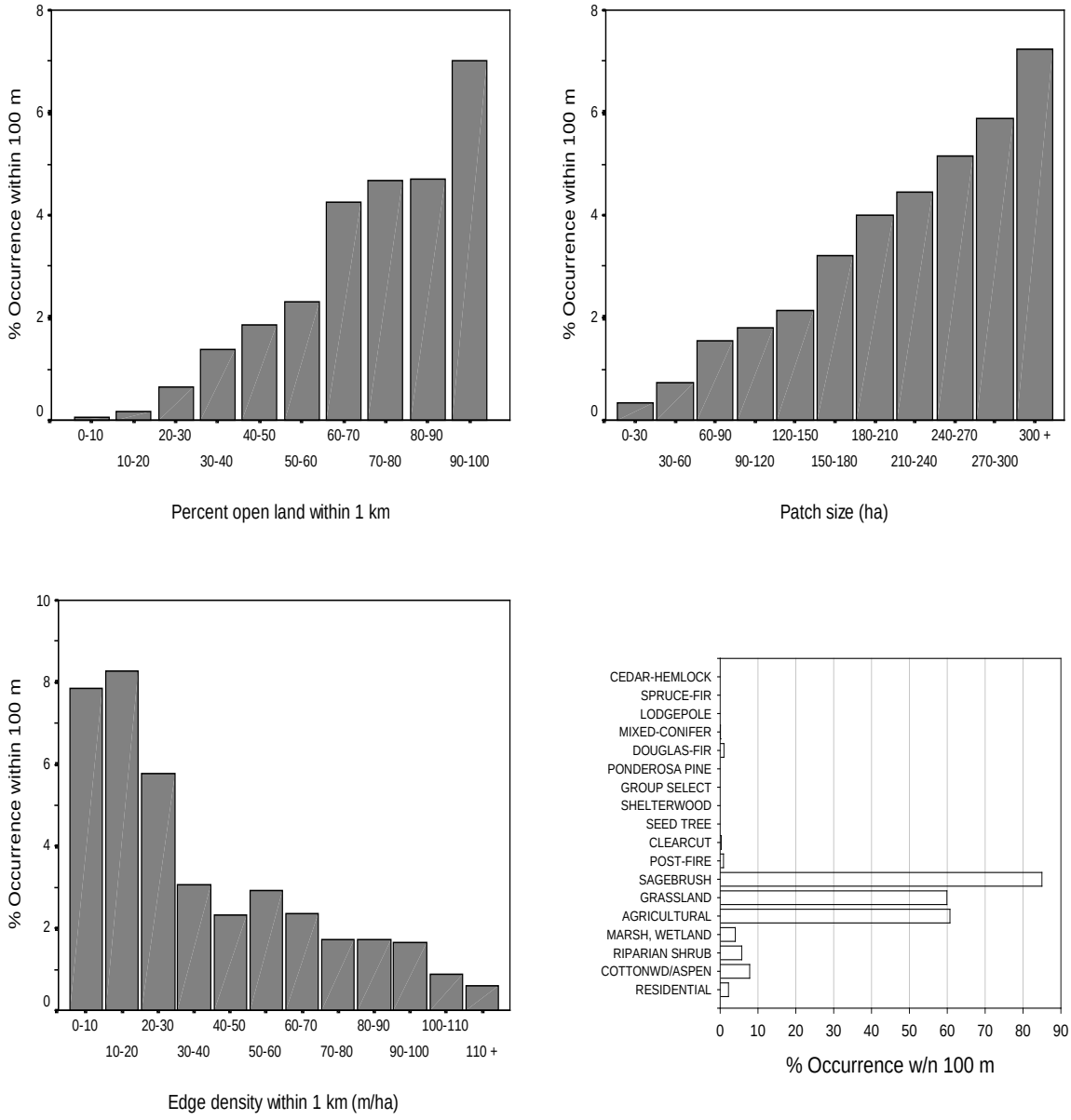


Figure 19. The presence of Vesper Sparrow was significantly associated with all three landscape variables, but some of the associateion is certainly an artifact of using open shrubland points in the analysis, as explained more fully in the discussion.

Savannah Sparrow

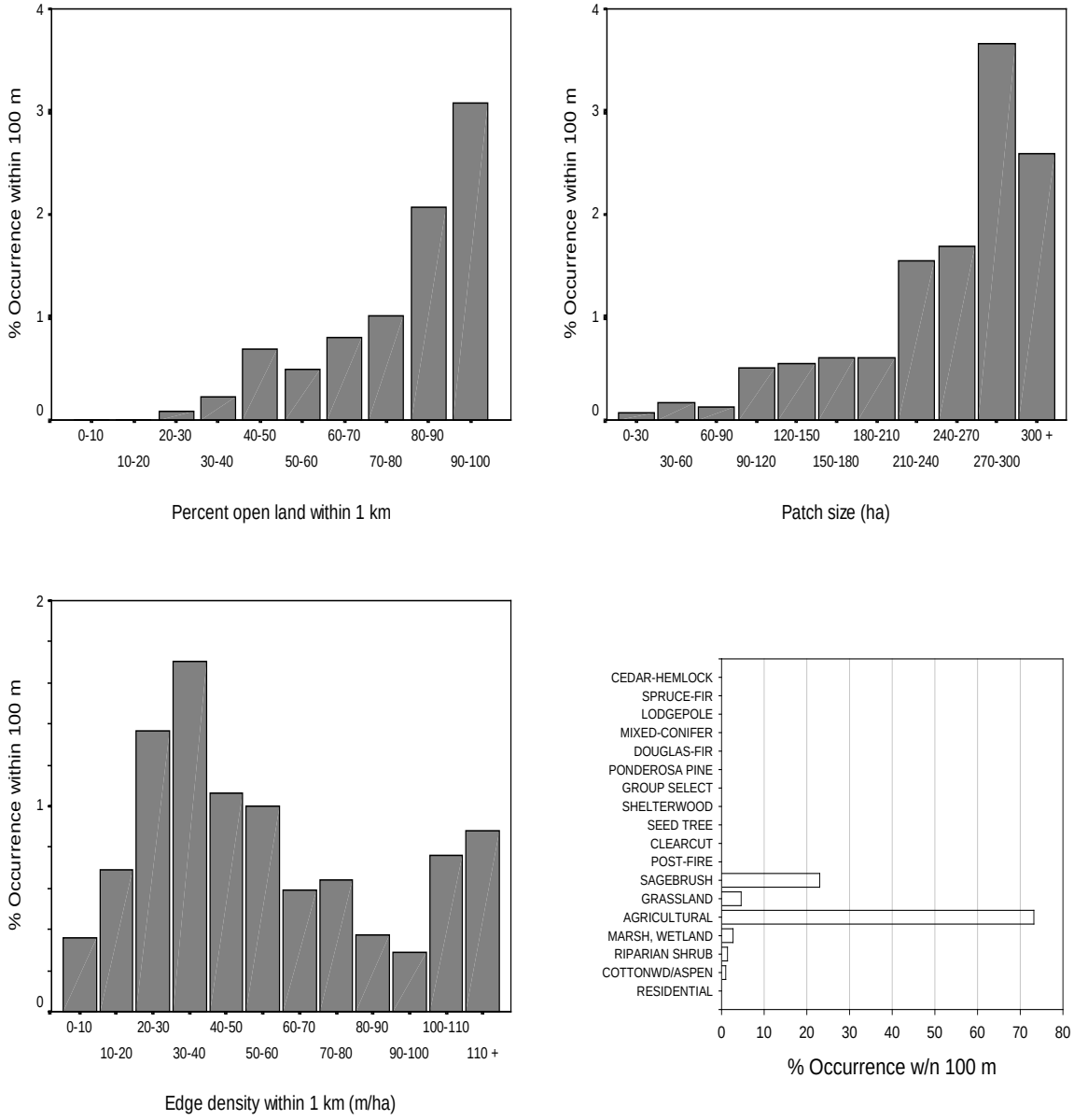


Figure 20. The presence of Savannah Sparrow was significantly associated with all three landscape variables, but some of the associateion is certainly an artifact of using open shrubland points in the analysis, as explained more fully in the discussion.

Grasshopper Sparrow

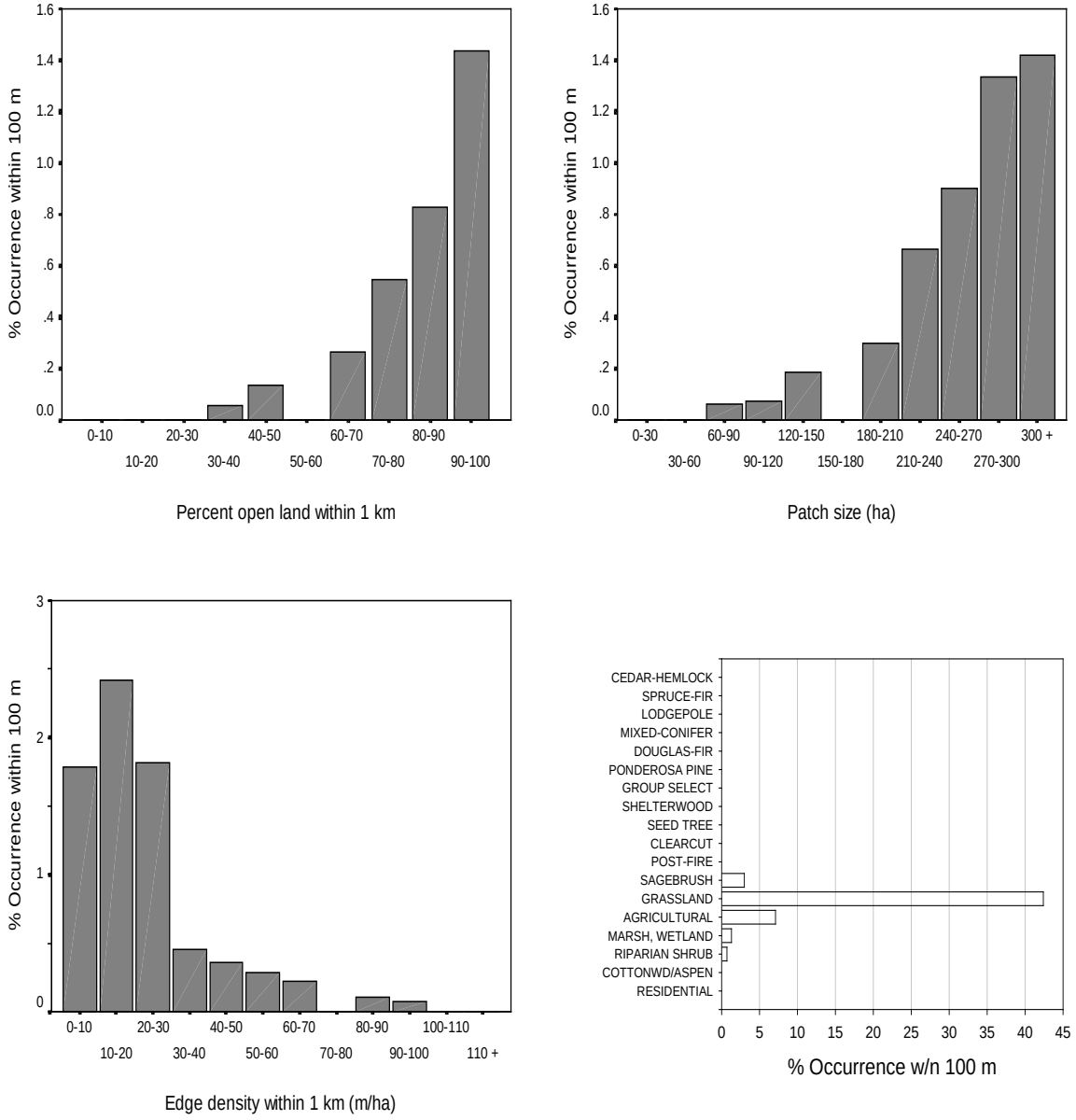


Figure 21. The presence of Grasshopper Sparrow was significantly associated with all three landscape variables, but some of the associateion is certainly an artifact of using open shrubland points in the analysis, as explained more fully in the discussion.

Brewer's Sparrow

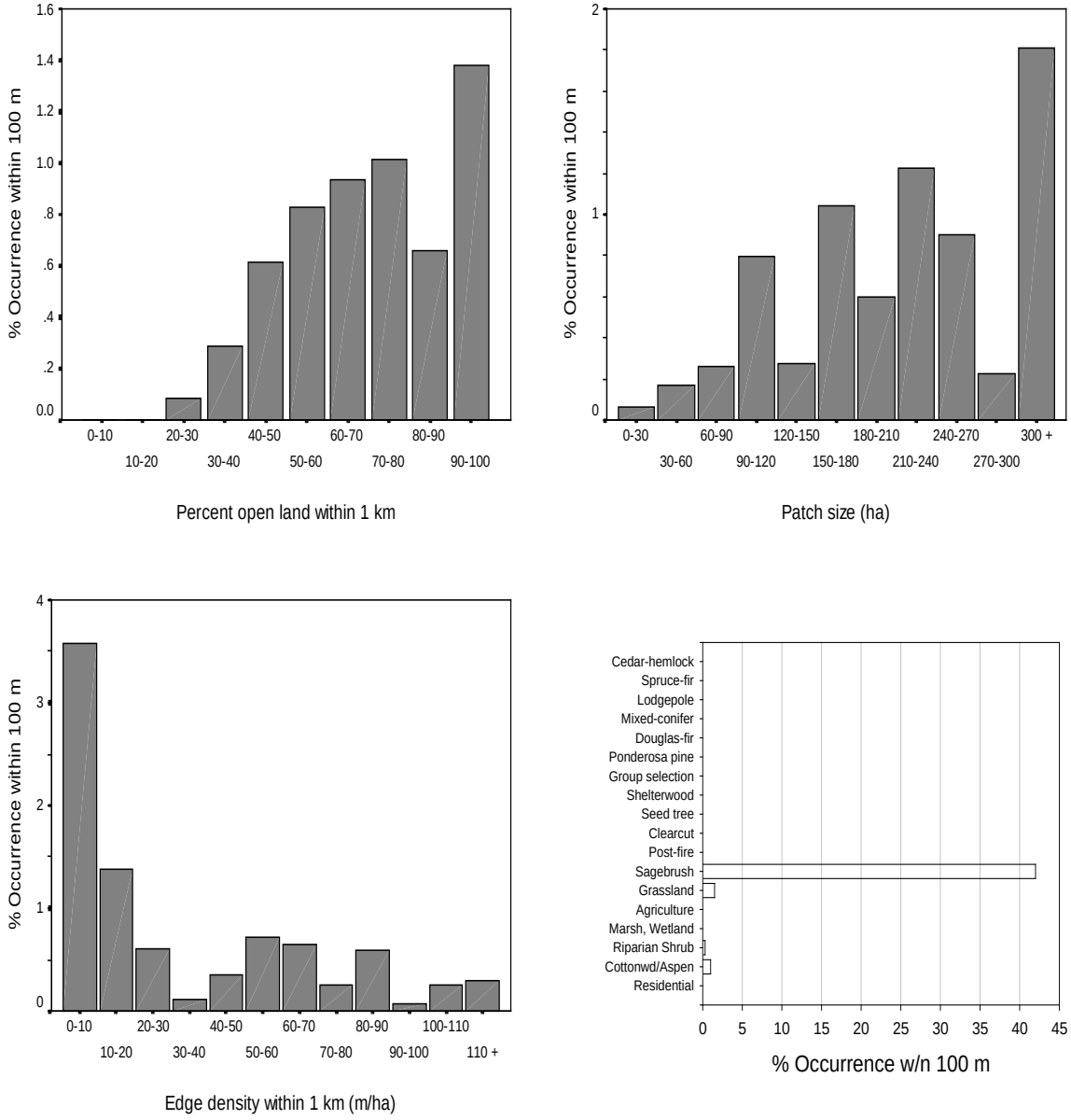


Figure 22. The presence of Brewer's Sparrow was significantly associated with all three landscape variables, but some of the associateion is certainly an artifact of using open shrubland points in the analysis, as explained more fully in the discussion.

Horned Lark

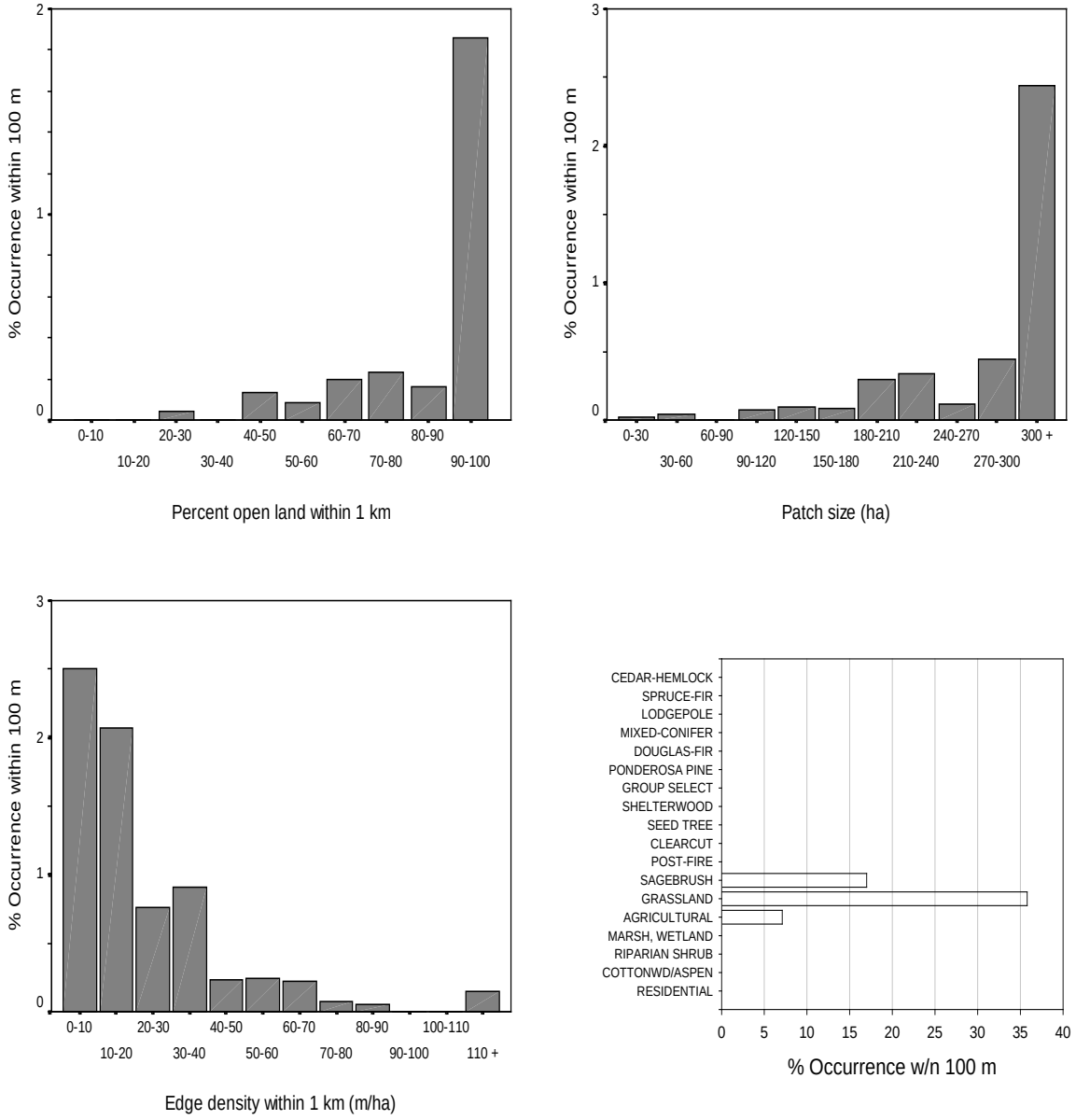


Figure 23. The presence of Horned Lark was significantly associated with all three landscape variables, but some of the associateion is certainly an artifact of using open shrubland points in the analysis, as explained more fully in the discussion.

Brewer's Blackbird

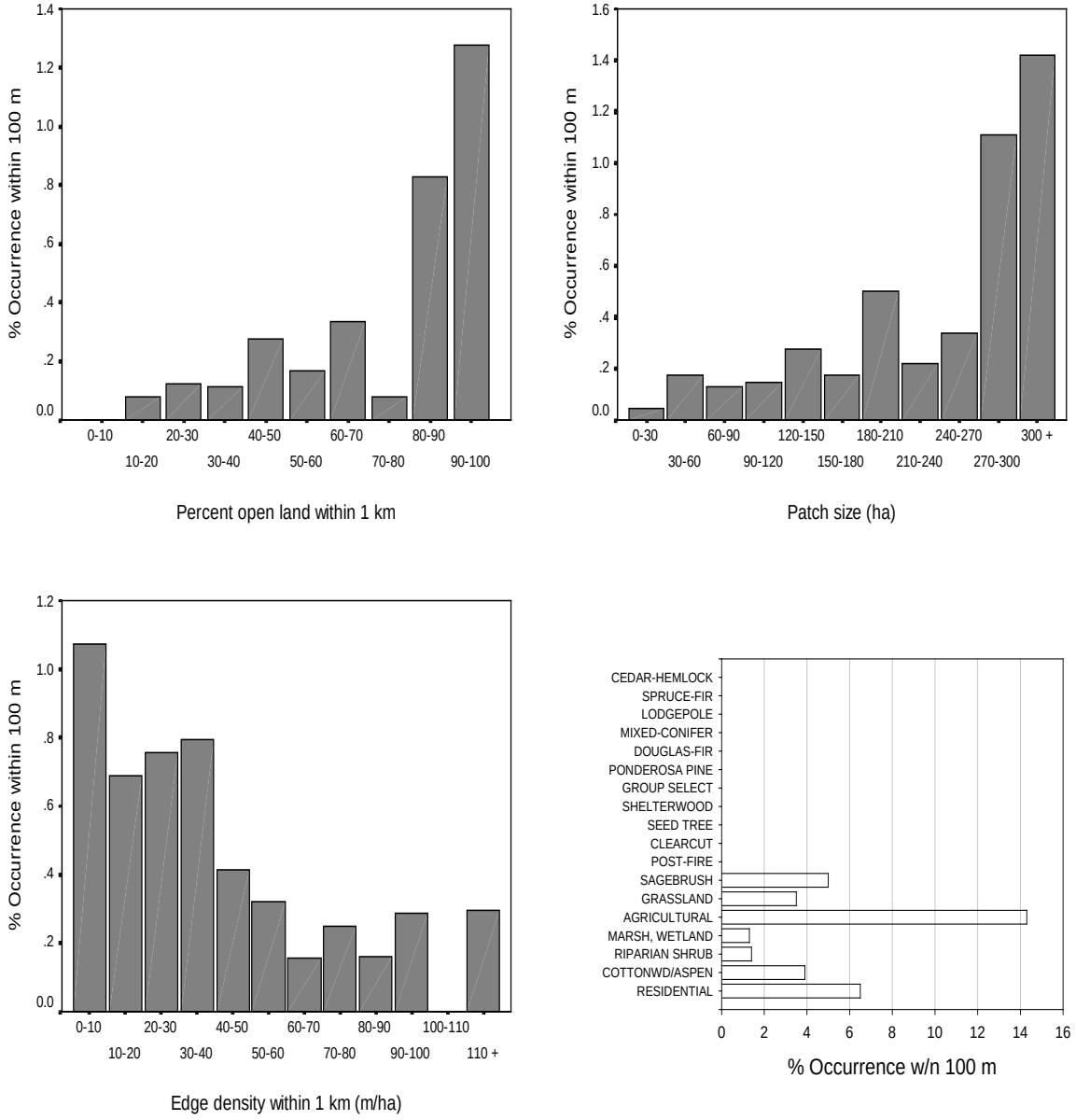
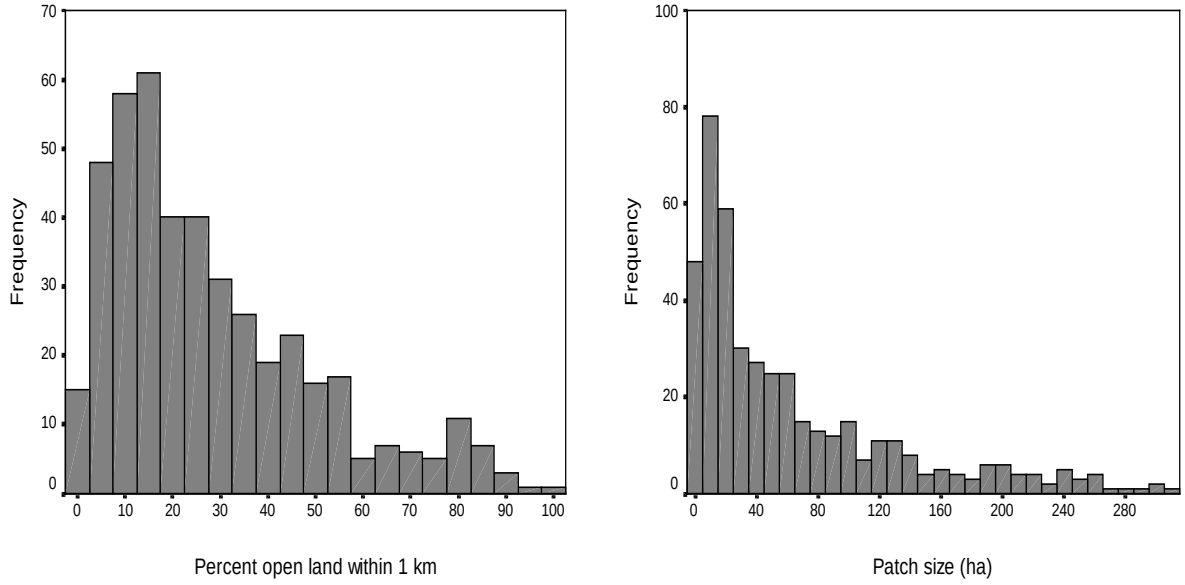


Figure 24. The presence of Brewer's Blackbird was significantly associated with all three landscape variables, but some of the associateion is certainly an artifact of using open shrubland points in the analysis, as explained more fully in the discussion.

Mesic Shrublands (including clearcuts)



Grasslands

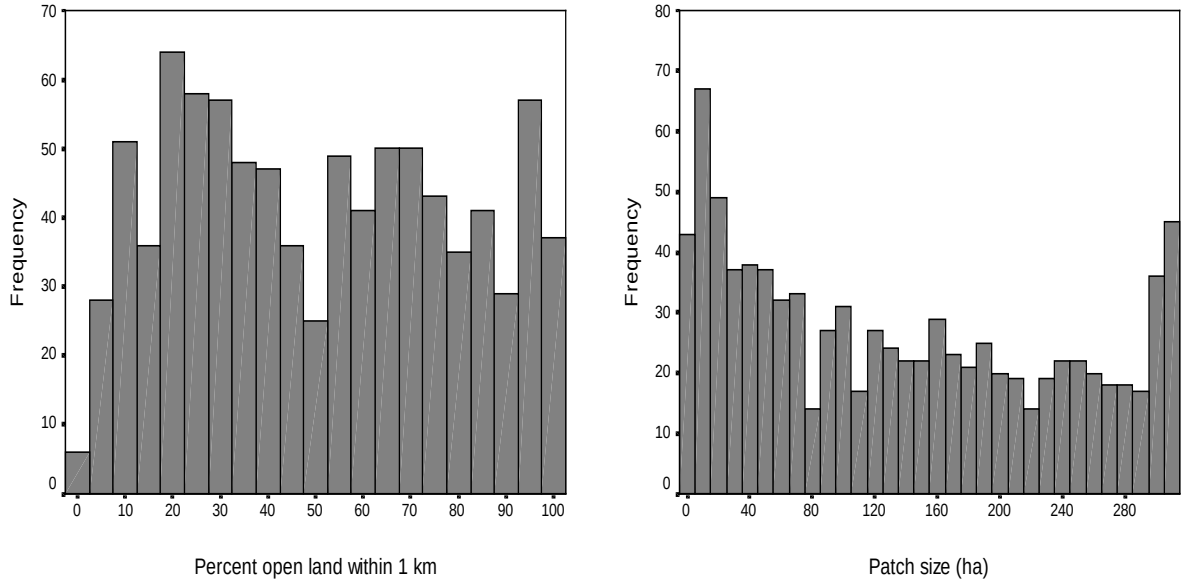


Figure 25. Frequency distributions of two landscape variables around points that fell within the "open land" cover type. The mesic shrub subset included clearcuts and occurred in less open landscapes, on average (28% open; n=440), than did the grassland subset of points (51% open; n=888). Mesic shrub patches also tended to be smaller than grasslands (mean patch sizes were 63 and 135 ha, respectively).